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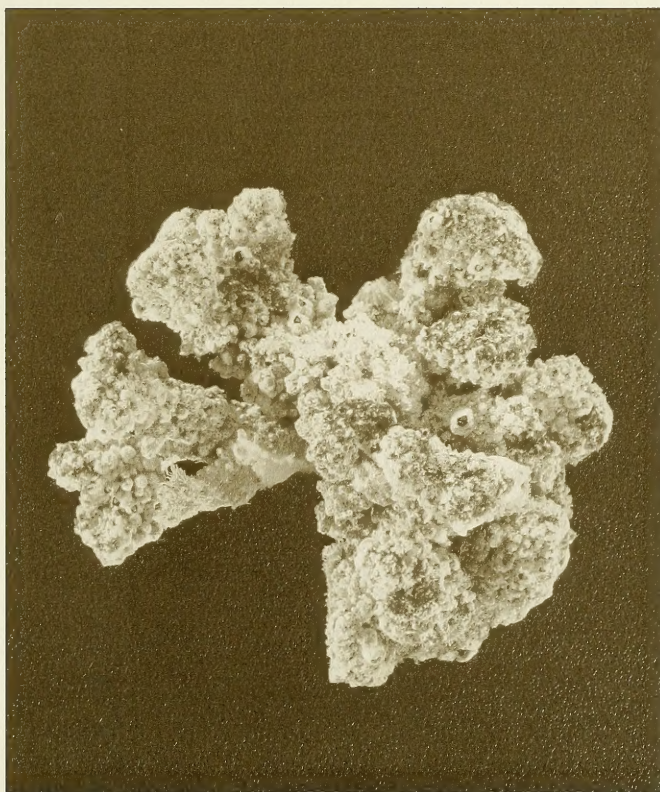
ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 89

Number 1



BCAS-A89(1) 1-48 (1990)

APRIL 1990

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

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Date of this issue 8 May 1990

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

Late Quaternary Nonmarine Mollusca from Kokoweef Cave, Ivanpah Mountains, California

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Abstract.—An assemblage of one freshwater and seven terrestrial mollusk species was collected in Kokoweef Cave, at 1720 m in the Ivanpah Mountains, San Bernardino County, California, associated with vertebrate remains of Rancholabrean (late Pleistocene) age. All but one of the molluscan taxa are extant. Most of the species indicate an environment like that of modern pine and fir forest now found at elevations above 2200 m in the Spring Range, Nevada. There is also a xerophilic element characteristic of the modern Lower Sonoran Zone. In the time interval represented by the fossils, the pine and fir forest zone probably extended 500–1000 m lower than at present.

A molluscan assemblage consisting of one freshwater and seven terrestrial species (Table 1) was collected in Kokoweef Cave, Ivanpah Mountains (NE1/4 NW1/4 sec. 4, T. 15 N, R. 14 E, San Bernardino Base and Meridian; elev. 1720 m), San Bernardino County, California, by parties from the San Bernardino County Museum (Loc. SBCM 1-11-13). They range from the 18.5 ft (5.6 m) to the 37–38 ft (11.3–11.6 m) datum of excavation and were associated with abundant vertebrate remains indicating a Rancholabrean (late Pleistocene) age.

Vertebrate fauna and flora from the cave that are extinct or locally absent include *Equus* sp., cf. *E. conversidens*; *Camelops* sp.; *Hemiauchenia* sp.; *Euceratherium?* sp.; *Canis* sp., cf. *C. dirus*; *Marmota flaviventris*; *Ochotona princeps*; *Spermophilus townsendi*; *Spermophilus lateralis*; *Tamias minimus*; *Tamias palmeri*; *Lagurus* sp.; *Gymnogyps* sp.; and *Celtis* sp. (Goodwin 1986; Reynolds 1972, San Bernardino County Museum collections). The reptile fauna has been reviewed by Norell (1986). A radiocarbon age of 9830 ± 150 yr BP has been obtained on charcoal from the 20.5 ft (6.2 m) datum (A. Sarna-Wojcicki, *in litt.* to Reynolds, June 26, 1985).

At present the vegetation in the environs of Kokoweef cave is juniper scrub, including *Ephedra* spp., *Yucca baccata*, and *Yucca schidigera*. There are no published records of the modern mollusk faunas of the Ivanpah Mountains or adjacent Mescal Range. In the better-studied Spring Range, Clark County, Nevada, 40–110 km to the north, land snails are largely restricted to the coniferous forest above 2200 m, with a few species ranging down to springs in pinyon-juniper woodland at 1900 m (Pratt 1976).

In analyzing a fossil assemblage, it is necessary to determine whether the constituent taxa could all have lived in the same habitat and whether they were

Table 1. Late Pleistocene nonmarine mollusks from Kokoweef Cave. Samples are deposited in the Earth Sciences Department, San Bernardino County Museum. Data are number of specimens/number of fragments. A "specimen" is defined as a whole shell or a piece of shell containing either the apex or the adult aperture (whichever is more numerous in the sample); all other pieces are considered "fragments."

Species	Occurrence									
	18-5'NW	21'NW	22-23'NW	23-24'NW	28-29'SW	29-30'SW	34-35'SW	37-38'SW		
Gastropoda										
<i>Tryonia protea</i> (Gould, 1855)		2/0	281/39	2/0	1/0					
<i>Gastrocopta pellucida hordeacella</i> (Pilsbry, 1890)		2/9	133/83	12/17	3/1	5/0	1/0		2/0	
<i>Pupilla hebes</i> (Ancey, 1881)		52/0	562/25	*	2/0	7/0	11/0		15/0	
<i>Vallonia cyclophorella</i> Sterki, 1892	1/0	15/0	87/0	*		8/0	6/0		6/0	
<i>Vallonia</i> , n. sp.?			40/4	12/5		5/0				
<i>Succinea</i> sp., cf. <i>S. gabbi</i> Tryon, 1866	2/1	7/0		1/0					3/0	
<i>Hawaiiia minuscula</i> auctt., non (Binney, 1840)		1/0		1/0					3/0	
<i>Oreohelix handi</i> Pilsbry, 1917	0/1	0/3	14/3	6/1	1/0	1/0	2/2			

* Total *Vallonia* present in sample 125/10; *V. cyclophorella* and *V. n. sp.?* not distinguished in sorting.

preserved in the environment in which they lived. California has no truly troglitic land mollusks (A. G. Smith 1957), although some may at times find the right conditions of moisture, shelter, and food availability near the mouths of caves. Except as discussed below, the mollusks in Kokoweef Cave probably washed or drifted in from habitats in the near vicinity. Like many of the bones in the deposit, some may have been brought in by wood rats (*Neotoma*). *Tryonia protea* is a freshwater snail; the others are terrestrial (or in the case of *Succinea*, perhaps marginally aquatic) species.

In addition, *T. protea* and *Gastrocopta pellucida hordeacella* are xerophilic forms, while the other species could readily represent a modern biocoenosis that would occur under cooler and moister conditions than those now present in eastern San Bernardino County at the elevation of Kokoweef Cave.

Modern Occurrence of Component Taxa

All taxa identified to species are extant; *Vallonia* n. sp.? may be extinct. *Tryonia protea* today occurs in scattered populations from western Utah to southeastern California and adjacent Baja California, in streams flowing out of thermal springs (Taylor 1981), but was formerly abundant in pluvial lakes, including Lake Cahuilla (Stearns 1883; Bowersox 1974). Typical modern occurrences would include those in limnocrenes and their outflow streams at Ash Meadows, Nye County, Nevada, and in Death Valley, California (W. L. Pratt, *in litt.* to Roth, 1986) in the Lower Sonoran Life Zone.

Gastrocopta pellucida hordeacella is widespread from the southern United States to Central America, reaching west to Snow Creek and Palm canyons, San Jacinto Mountains, Riverside County, California (Berry 1922; Roth, unpublished data). Its broad geographic range implies considerable eurytopy, but little ecological information has been published. In Arizona and New Mexico it is common in the Lower and Upper Sonoran life zones from elevations of 300 to 2000 m (Bequaert and Miller 1973; Ashbaugh and Metcalf 1986). The San Jacinto Mountains occurrences are also in the Lower Sonoran Zone. The species occurs in spring-fed marshes in Clark County, Nevada, but only below 700 m (W. L. Pratt, *in litt.* to Roth, 1986). In New Mexico it is "common in leaf litter under shrubs along floodplains and in lower canyons in mountainous areas" (Ashbaugh and Metcalf 1986:10).

Pupilla hebes is a characteristic Rocky Mountain and Great Basin species. Its present distribution extends from Montana, at an elevation of 1200 m, to northern Chihuahua at 2100 m and Baja California at 2700–2800 m (Miller 1981). In Arizona it ranges from 1500 to 3400 m (Bequaert and Miller 1973). Typical habitats range from mixed aspen-conifer woodland, on the mesic extreme, to the more xeric pine-locust or oak-juniper woodland (LaRochelle 1986). In the central Great Basin, Pratt (1979b) reports it as sporadic in rockslides and burrowing along rock ledges. The species has not been reported previously from San Bernardino County, California, but it has been collected at the following California localities: 7.2 km southeast of Markleeville, Alpine County, by W. L. Pratt, June 1978; along Lee Vining Creek, West Walker River at U.S. Highway 395, and Silver Lake, all in Mono County, by W. B. Miller, July 1985; and at 3000 m elevation in the Ancient Bristlecone Pine Forest, White Mountains, Mono and Inyo Counties, by W. B. Miller, 1985. The S. S. Berry molluscan collection at the Santa

Barbara Museum of Natural History contains one lot labeled Mono County, March 1940.

Vallonia cyclophorella ranges from the Dakotas to Arizona and southeastern California. In Arizona it ranges from 1400–3000 m, in the Transition, Canadian, and Hudsonian life zones (Bequaert and Miller 1973); in New Mexico, from 1950–3255 m in wooded canyons and montane forests (Ashbaugh and Metcalf 1986). In southern California it occurs over a similar range of altitudes and is found in forest litter and under logs or bark on the ground. In the Spring Range it is restricted to 1900 m and above (Pratt 1976). *Vallonia cyclophorella* is one of the most widely distributed species in the central Great Basin (Pratt 1979), occurring in all habitats supporting snails. The eurytopy limits its usefulness as an indicator of paleoenvironments.

In most of the samples, another form of *Vallonia* is present, usually in smaller numbers than *Vallonia cyclophorella*. It is larger than *V. cyclophorella* (to 3 mm in diameter), with four whorls. The body whorl expands less rapidly than in *V. cyclophorella* and turns down less sharply behind the aperture; the peristome is only weakly developed into a flange. This form (cited as *Vallonia* n. sp.?) may be extinct; it cannot be identified with any species known to be living in North America. We draw no paleoenvironmental inferences from it at this time.

Empty shells of the family Succineidae, such as *Succinea* sp., cf. *S. gabbi* reported here, cannot usually be identified to species. In general, however, succineids are snails of moist habitats, such as the edges of marshy lakes or moist mountain meadows. *Succinea gabbi* is known from the Great Basin drainage of California and from eastern Oregon and Washington.

Hawaiiia minuscula is a eurytopic and widely distributed species, at present ranging from Alaska and Newfoundland to Central America. Records of the species from the arid southwest, however, pertain to one or more anatomically distinct, unnamed species (Pratt 1979, and unpublished report to Desert Research Institute, University of Nevada). In southern Nevada, *Hawaiiia minuscula* auctt. occurs in damp, grassy areas around springs and along permanent streams in the lower montane zone (Pratt, unpublished). In Arizona it ranges from 800 to 2600 m (Bequaert and Miller 1973). In western Texas and New Mexico, it occurs on floodplains, in mesic, forested montane habitats, and in relatively xeric habitats in low mountains and foothills (Ashbaugh and Metcalf 1986).

Oreohelix handi is restricted at present to the Spring Range, Nevada, at elevations of 2700–2900 m on Charleston Peak and at 2300 m on Potosi Mountain (Pilsbry 1939; Pratt 1976). These localities are in the zones of White Fir, Limber Pine, and the upper range of Yellow Pine (Mehringer 1964), equivalent to the Transition Zone and the lower part of the Canadian Zone. W. L. Pratt (*in litt.* to Roth, 1986) reports that *O. handi* is found “only in the pine-fir conifer forest, but is apt to turn up in any little patch of the habitat where there is a sheltered slope or some ledges, even though the surrounding slopes are in pinyon-juniper woodland. It is generally found under small rocks, logs and similar cover.”

A similar but larger-shelled species, *Oreohelix jaegeri* Berry, 1931 (not a subspecies of *O. handi* as it was formerly regarded [Pratt 1979a]), occurs at 2300 m on Charleston Peak, but the Kokoweef Cave specimens more closely resemble *O. handi*. This is the first record of *O. handi* outside of Nevada. The occurrence in Kokoweef Cave is 60 km south of its present range. The only Recent occurrence

of *Oreohelix* in California is that of *Oreohelix californica* Berry, 1931, on Clark Mountain, 15 km northwest of the Ivanpah Mountains, among limestone fragments and fir needles in rockslides at an elevation of 2100 m.

Interpretation of the Assemblage

Oreohelix handi is the most stenotopic species in the assemblage and therefore the most informative. It is also the most critical indicator of montane-type conditions. Its presence suggests that conditions now characteristic of pine and fir forest extended between 500 and 1100 m lower than their present elevation in neighboring ranges of southwest Nevada. The occurrences of *Pupilla hebes*, *Hawaiiia minuscula* auctt., and *Vallonia cyclophorella* are consistent with this interpretation, although the modern ranges of all three extend to lower altitudes elsewhere. All probably lived in the immediate vicinity of the cave, in relatively mesic, rocky sites. In a pine or fir forest setting, *Succinea* would be expected along the edges of low-gradient streams or in moist meadows.

Gastrocopta pellucida hordeacella probably occupied relatively xeric sites nearby; less likely, it may have been passively transported from a lower vegetation zone. It may have been an inhabitant of a biotope not now represented in the arid southwest—exposed grassy slopes, its suggested modern habitat in the High Plains (Franzen and Leonard 1947; Taylor 1960).

The association of *Gastrocopta pellucida hordeacella*, *Pupilla hebes*, *Hawaiiia minuscula* auctt., and *Vallonia cyclophorella* also occurs at Pleistocene sites in San Pedro Valley, Arizona, associated with mammoth remains 10,000–11,000 yr old (Bequaert and Miller 1973). The ecological amplitude of *G. p. hordeacella* may have overlapped those of *P. hebes* and *V. cyclophorella* during late Pleistocene times of greater moisture availability and less extreme summer temperatures. Floristic associations without modern analogues occur in late Pleistocene packrat middens in the Southwest (Ven Devender and Spaulding 1979), and owe their existence to the individualistic response of plant species to climatic change.

Tryonia protea is probably best interpreted as indicating a shallow pluvial lake outside the Ivanpah Mountains. Alternatively, it might have lived in the outflow of a thermal spring within the range itself, although no such spring is known. Pluvial lakes existed both east and west of the cave site (Hewett 1956; Reynolds and Jefferson 1971), contemporaneous with maximum late Pleistocene extension of woodland across the eastern Mojave Desert (Mehringer 1967: fig. 38). Their existence is compatible with the conditions that would depress the elevation of vegetation zones. Searles Lake rose to its maximum height 10,000–11,000 yr BP (G. I. Smith 1968). The bones of cyprinid fishes also occur in the Kokoweef Cave deposit. *Tryonia protea* may have been in the stomachs of fish not indigenous to the cave. Pupfish (Cyprinodontidae) and stickleback (Gasterosteidae) have been named as possible predators on other species of *Tryonia* (Kellogg 1980). Many species of shore and wading birds also include small mollusks in their diets.

Discussion

Numerous paleobotanical studies have indicated that during late Pleistocene (Wisconsinan) time, vegetation zones in the Mojave Desert and southern Nevada were as much as 1000 m lower in elevation than they are now (e.g., Mehringer 1966; Wells and Berger 1967; Van Devender 1977). Mammals from a cave in the

Mormon Mountains, Nevada, suggest that pine and fir floras were at least 600–900 m lower in elevation about 10,000 yr BP (Jefferson 1982). The upward shift of vegetation zones to their modern altitudes is mainly the result of climatic warming beginning in the “early Holocene xeric woodland period,” 8000–11,000 yr BP (Van Devender and Spaulding 1979).

At the same time that vegetation zones were lower, the ranges of many mammals and plants extended farther south than they do now (Van Devender and Spaulding 1979; Jefferson 1982). The southernmost present occurrence of *Oreohelix handi* is approximately 60 km north of its late Pleistocene occurrence in Kokoweef Cave. With the possible exception of *Succinea* sp., cf. *S. gabbi*, however, the other extant mollusks are within their modern geographic ranges.

Two geographically nearby fossil assemblages, at Valley Wells and Tule Springs, contrast significantly to the Kokoweef Cave assemblage (Table 2). Although these deposits are not precisely correlated, the differences in molluscan composition are explicable in terms of setting, with the Kokoweef Cave site representing uplands, and the other two sites lowland basins with more or less perennial bodies of water.

Taylor (1967) described late Pleistocene mollusks from the Tule Springs site, near Las Vegas, Nevada. The fossil pollen record from Tule Springs indicates that before about 12,000 yr BP the present low-elevation desert supported vegetation types ranging from higher-elevation desert to yellow pine parkland (Mehring 1964, 1967); at their maximum depression, vegetation zones were 1000–1200 m lower than at present. At least nineteen freshwater species, both bivalves and gastropods, are present, indicating a complex aquatic environment. Although the eurytopic *Vallonia cyclophorella* and *Hawaiiia minuscula* auctt. are present, the land mollusks represent a marshy-ground association quite different from the Kokoweef Cave assemblage. *Vertigo berryi*, for instance, has been found living in marshes along the Muddy River, Clark County, Nevada (Pratt 1979). *Gastrocopta tappaniana* occurs among moist leaves or under logs in moist grass near seepages (Taylor 1960) and on shaded slopes near streams (Franzen and Leonard 1947) in the High Plains. Both *V. berryi* and *G. tappaniana* are found in moist areas around springs in pinyon-juniper woodland in the lower elevations of the spring Range (W. L. Pratt, *in litt.* to Roth, 1986). Although the Tule Springs deposit was formed over a considerable time interval and the lowest levels may be pre-Wisconsinan, a specific assemblage of species spans the entire time represented by the fossiliferous strata and indicates the presence of small, shallow creeks or the marshy area of a seepage (Taylor 1967).

Hewett (1956) reported an assemblage of freshwater and land mollusks from Quaternary lacustrine beds near Valley Wells, San Bernardino County, 20 km west of the Ivanpah Mountains (Table 2). Mammals of Late Pleistocene age have been recovered from the deposit (Reynolds and Jefferson 1971). Both the stratigraphic setting and the fauna indicate deposition in a wet lowland basin. Tuff from Valley Wells lacustrine sediments north of Cima Dome are chemically correlated with ash beds elsewhere in the western states dated at 2 million and 0.6 million yr BP (A. Sarna-Wojcicki, *in litt.* to Reynolds, 1985), indicating a pre-Wisconsinan age.

Jefferson (1982) has cautioned against attempting to use simple elevational displacement of floristic elements to infer the age of a fossil assemblage, since

Table 2. Comparison of Kokoweef Cave mollusks with terrestrial mollusks from late Pleistocene assemblages from Valley Wells, California, and Tule Springs, Nevada, and Recent native land mollusk fauna of Spring Range, Nevada. Freshwater components of fossil assemblages summarized.

Species	Occurrence			
	Kokoweef Cave (this report)	Valley Wells (Hewett, 1956)	Tule Springs (Taylor, 1967)	Spring Range (Pratt, 1976 ¹)
Terrestrial				
<i>Gastrocopta pellucida hordeacella</i> (Pilsbry)	X	—	—	—
<i>Gastrocopta tappaniana</i> (C. B. Adams)	—	—	X	X
<i>Pupilla blandi charlestonensis</i> Pilsbry	—	—	—	X
<i>Pupilla hebes</i> (Ancey)	X	—	—	—
<i>Pupilla</i> , n. sp.	—	X	—	—
<i>Pupilla</i> , sp. indet.	—	—	X	—
<i>Vertigo berryi</i> Pilsbry	—	X	X	X
<i>Vertigo gouldii</i> (Binney)	—	—	—	X
<i>Vertigo modesta ingersolli</i> Cockerell	—	—	—	X
<i>Vertigo</i> sp. indet.	—	X	—	—
<i>Vallonia cyclophorella</i> Sterki	X	X	X	X
<i>Vallonia gracilicosta</i> Reinhardt	—	—	X	—
<i>Vallonia</i> , n. sp.?	X	—	—	—
<i>Discus cronkhitei</i> (Newcomb)	—	—	—	X
<i>Oxyloma</i> sp.	—	—	X	—
<i>Catinella stretchiana</i> (Bland)	—	—	—	X
<i>Succinea</i> sp., cf. <i>S. gabbi</i> Tryon	X	—	—	—
<i>Succinea avara</i> auctt., non Say	—	X	—	X
cf. <i>Succinea</i> , 2 spp.	—	—	X	—
<i>Euconulus fulvus</i> (Müller)	—	—	—	X
<i>Vitrina pellucida</i> (Müller)	—	—	—	X
<i>Hawaiiia minuscula</i> auctt., non Binney	X	—	X	X
<i>Deroceras</i> sp., cf. <i>D. laeve</i> (Müller)	—	X	—	X
<i>Oreohelix handi</i> Pilsbry	X	—	—	X
<i>Oreohelix jaegeri</i> Berry	—	—	—	X
Freshwater (summary)				
<i>Tryonia protea</i> (Gould)	X	—	—	
Other Hydrobiidae	—	—	2 spp.	
Valvatidae	—	—	1 sp.	
Lymnaeidae	—	2 spp.	5 spp.	
Ancylidae	—	—	1 sp.	
Planorbidae	—	1 sp.	4 spp.	
Physidae	—	—	1 sp.	
Sphaeriidae (Bivalvia)	—	1 sp.	5 spp.	

¹ With additions from Pratt, in litt., 1986.

plant species tend to respond to climate changes individualistically rather than as communities (Van Devender and Mead 1976). The caveat may be underscored for mollusks as well, since microhabitat conditions rather than the taxonomic composition of the flora determine their local distribution. Moreover, both land and freshwater mollusks are well known for tending toward relict distributions, which, if not recognized as such, may obscure, rather than cleanly reflect, the broad climatic trend at a given time.

Acknowledgments

We are grateful to P. B. LaRochelle, W. B. Miller, and W. L. Pratt for comments on various parts of the manuscript and for permission to cite unpublished data from their own studies. M. G. Kellogg suggested to Roth the possibility that *Tryonia protea* was introduced to the deposit in stomachs of fish transported to the cave by birds.

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Accepted for publication 28 November 1988.

Movement and Habitat Selection in Tagged Rock Crabs (*Cancer antennarius*) in Intertidal Channels at James V. Fitzgerald Marine Life Refuge, California

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Abstract.—From November 1987 to February 1989, 387 rock crabs (*Cancer antennarius*) were tagged in three intertidal channels at James V. Fitzgerald Marine Life Refuge. Searches for crabs were conducted in the channels during low tides at least monthly. Seventy-nine crabs were resighted alive, 70 of these within one month of tagging. The other nine were resighted at two to nine months after tagging. Seven were resighted more than once. All were resighted in the channels in which they were tagged. Twelve were found dead, all within a short distance of the channels.

Tagged *C. antennarius* measured 71–133 mm in carapace width. The sex ratio was skewed toward females, particularly in spring and summer, but few ovigerous females were found. Eighty-two crabs (21%) were missing or regenerating appendages, six had cracks or holes in the carapace, and twenty-four were encrusted with coralline algae or barnacles. Only one crab was resighted after healing from a previously observed injury. No tagged crab molted during the study period.

The crabs seem to use the channels in moving between the intertidal zone and adjacent subtidal areas. Shelter is important to the crabs, which rarely move during low tides.

Rock crabs (*Cancer antennarius*) are among the largest intertidal crabs in central California. Although not sufficiently common to support a major fishery, they are taken at times by commercial fishermen, divers and sport fishermen. They are important predators on shelled mollusks and small crustaceans, which they crush with their powerful chelae (Garth and Abbott 1980).

Studies on size and seasonal abundance of adult and juvenile *C. antennarius* were conducted in intertidal channels at James V. Fitzgerald Marine Life Refuge (also known as James V. Fitzgerald Marine Life Reserve), San Mateo County, California (Fig. 1) during 1985 and 1986 (Breen and Wicksten 1988). The crabs were consistently found in the channels, but relative abundance was lowest after severe winter storms. Male to female sex ratio was 1.6:1. Juveniles were most abundant from late summer through the fall. Individual crabs were recognizable by characteristic injuries, scars, and fouling organisms, but only rarely was the same recognizable individual crab seen during the monthly observations in the channels.

To find out more on the movements, size and sex ratio of the crabs, a tagging

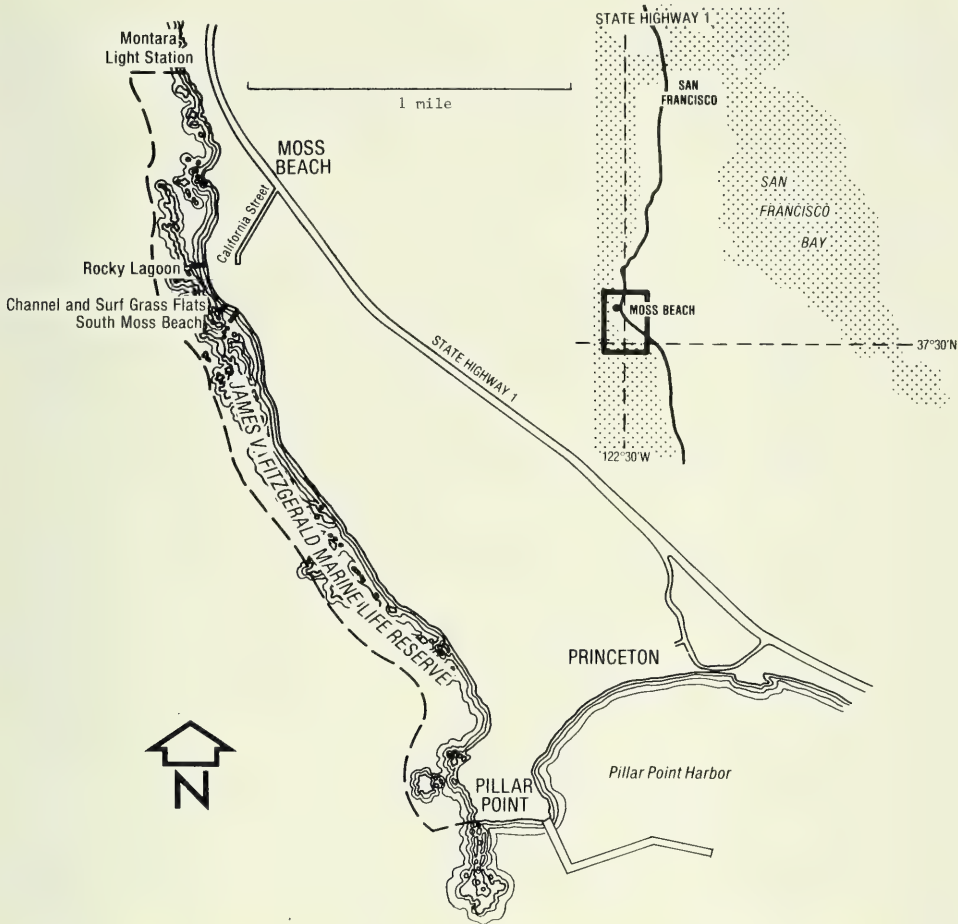


Fig. 1. Map of study area. (The Refuge also is called James V. Fitzgerald Marine Life Reserve on many maps).

study was conducted from November 1987 to February 1989. The objectives were to track movements of the crabs in the intertidal zone, examine habitat preference, and document sex ratios, sizes, seasonal abundance, and crab condition (injuries and fouling). The results provide information on free-ranging crabs in their natural habitat in the intertidal zone.

Materials and Methods

From 19 November 1987 to 16 February 1989, 387 rock crabs were tagged in three intertidal channels in the flat shale reef at the Refuge (Fig. 1). Each channel varied in width, but was bordered by the shale reef which rises at least 0.3 m above the level of each channel. All of the channels were submerged during tides of 0.8 m or greater. The first channel ("Rocky Lagoon") was broad (up to 20 m wide) and covered with movable rocks and boulders. A 50 m transect was established in the shoreward half of the area of the channel. The second transect ("Channel and Surf Grass Flats") was 50 m long by 5 m wide, and consisted of a rock-covered surge channel with a direct connection to the ocean during all tidal

phases. This channel extended higher in the intertidal zone (to the 0.8 to 0.0 tide levels) than the other study sites, and could be exposed to air and visitor disturbance more so than the other two channels. The third transect ("South Moss Beach") was located in a surge channel off south Moss Beach at the 0.0 to -1.0 foot tide level in surf grass (*Phyllospadix* sp.) flats. This channel was narrow and consisted mainly of a 42 m long crevice, as deep as 40 cm, that ran nearly the length of the transect. Each channel was separated from neighboring channels by at least 300 m of rocky reef.

For purposes of this study, transect lines were located in areas known to be inhabited by rock crabs that were accessible to observers. Each transect line was measured from meter 00 (closest to the beach) and extended seaward and lower into the intertidal zone to meter 50. Rock crabs were located within each transect using a line intercept method with the x-axis being the transect line itself and the y-axis a line drawn perpendicular to the transect line and out to the crab's location. Crabs were captured, tagged, and released in the exact location and position (on the surface, in a crack, buried, etc.) where they were discovered.

Searches for rock crabs were conducted at least once per month when possible and observations were made when tides were generally lower than 0.0 feet (mean lower low water level). Particular attention was paid to habitats in which crabs were found previously, including cracks and sandy areas beneath large rocks, which were lifted during searches (Breen and Wicksten 1988). Crabs were tagged with Floy tag #FD 67, 62 mm (2.5 inches) long, monofilament with a #20 bright orange tube bearing the legend San Mateo Co. Parks 000, and numbered sequentially. Tags were inserted into the right epimeral suture line above the second and third ambulatory legs with a Floy Mark II tagging gun, using a Mark II "Swiftacher" 1.85 mm tagging needle. Only crabs over 70 mm wide were tagged. Newly-molted crabs were not tagged because they proved to be too fragile—appendages were lost and the carapace was damaged when one attempted to insert the tagging needle.

During the study, the following data were collected for each individual: location (transect and location within the transect), tag number (if previously tagged), carapace width (measured in millimeters across the carapace between the ninth and tenth anterolateral teeth), sex, type of shelter used by the crab, female reproductive condition, damage to the crab, and any fouling.

Results

The sex ratio and numbers of crabs per carapace width interval at each channel is given in Tables 1–3. Three hundred eighty-seven rock crabs were tagged. The smallest measured 71 mm, the largest was 133 mm.

The sex ratio of the crabs was highly skewed toward females, particularly in spring and summer. However, ovigerous females were rarely found at any time: only eight were tagged; another six (not tagged) were observed on 16 February 1989.

Almost all of the crabs (97%) were found under rocks or in deep crevices. There was no sign of a shift in habitat preference in recaptured crabs—those originally found under a rock almost always were recaptured under a rock; those in a crevice usually were relocated in a crevice. Six crabs were found hidden under sea grasses,

Table 1. Sex and carapace width of *Cancer antennarius* at Rocky Lagoon, Fitzgerald Marine Reserve.

Month	Sex		70-79 mm	80-89	90-99	100-109	110-119	120 and larger	Comments
	M	F							
November 1987	3	3	2	1	1	1	—	1	
December	7	2	1	4	4	—	—	—	
January 1988	7	11	—	7	4	5	2	—	
February	6	4	—	—	2	2	4	2	
March	2	4	—	1	1	2	1	1	
April	2	5	—	—	1	1	4	1	
May	2	1	—	—	2	—	—	1	
June	5	13	—	2	9	1	5	1	
July	—	2	—	2	—	—	—	—	
August	—	—	—	—	—	—	—	—	Not visited
September	1	3	—	—	—	3	—	1	
October	2	4	—	—	3	3	—	—	
November	—	—	—	—	—	—	—	—	High surf
December	2	2	—	—	3	—	—	1	
January 1989	3	3	—	—	2	3	1	—	
February	7	4	—	—	3	4	4	—	
Totals	49	61	3	17	35	25	21	9	

Sex includes all crabs tagged each month. Numbers per size range are numbers of individuals per size measured in millimeters across the widest part of the carapace.

Table 2. Sex and carapace width of *Cancer antennarius* at channel and surf grass flats, Fitzgerald Marine Reserve.

Month	Sex		70-79 mm	80-89	90-99	100-109	110-119	120 and larger	Comments
	M	F							
November 1987	—	—	—	—	—	—	—	—	Not visited
December	7	7	3	2	2	6	1	—	—
January 1988	3	9	3	1	4	4	—	—	—
February	2	8	—	3	2	2	1	2	—
March	5	4	—	3	2	2	—	2	—
April	—	—	—	—	—	—	—	—	No crabs found
May	—	2	—	—	—	1	1	—	—
June	1	3	—	—	2	2	—	—	—
July	2	4	—	—	2	3	1	—	—
August	—	5	—	—	—	1	1	3	—
September	—	—	—	—	—	—	—	—	Not visited
October	—	4	—	—	2	—	2	—	—
November	—	—	—	—	—	—	—	—	High surf
December	—	2	—	—	—	1	1	—	—
January 1989	1	2	—	—	2	1	—	—	—
February	3	1	—	—	—	2	2	—	—
Totals	24	51	6	9	18	25	10	7	—

Table 3. Sex and carapace width of *Cancer antennarius* at South Moss Beach, Fitzgerald Marine Reserve.

Month	Sex		70-79 mm	80-89	90-99	100-109	110-119	120 and larger
	M	F						
November 1987	—	—	—	—	—	—	—	—
December	6	1	—	2	3	1	—	1
January 1988	8	6	—	1	5	3	2	3
February	2	6	—	—	—	4	3	1
March	7	17	—	—	4	7	10	3
April	3	6	—	—	2	3	2	2
May	2	12	—	—	2	5	4	3
June	8	16	—	—	2	10	10	2
July	8	14	—	—	1	12	7	2
August	—	3	—	—	—	1	1	1
September	1	10	—	—	1	7	2	1
October	2	16	—	—	—	9	7	2
November	1	9	—	—	2	4	3	1
December	6	18	—	—	5	7	10	2
January 1989	3	4	—	—	2	1	4	—
February	—	5	—	—	—	4	1	—
Totals	57	143	0	3	29	78	66	24

three were buried in sand or gravel, and two were ranging freely in the open in tide pools.

Eighty-two crabs (21%) were missing or regenerating appendages: 25 were missing one chela, three were missing both chelae, 22 were missing one or more walking legs, six were missing a chela as well as one or more legs, and the remainder were missing parts of appendages or their injuries were not specified. Six had holes or cracks in the carapace. Nineteen were encrusted with coralline algae, five had barnacles attached to the carapace. The injured and encrusted crabs were represented proportionally to their size frequency in the population—there was no indication of increased injury or fouling with larger crab size. Only one tagged crab (#18) showed evidence of healing from a previous injury in which the carapace was cracked. None of the tagged crabs had molted when recovered.

Seventy *C. antennarius* (18%) were sighted alive again after tagging (Table 4). Of these, all but nine were rediscovered within five weeks after their initial tagging. Six were found within six months after tagging, two after six months, and one after nine months. One crab was sighted after an absence of two months, then found again 13 days later. All but one of the crabs absent for more than five weeks were resighted in the same transect in which it originally was tagged.

Seven crabs were resighted more than once (Table 4). All of these crabs were resighted in the same transect in which they were originally tagged.

Movement of the crabs within a channel was frequent. Movements of tagged crabs from their original location were approximately equal landward (35 recaptures) versus seaward (36 recaptures), with 11 recaptures in approximately the same place. The maximum net distance moved per day per crab was 16.4 m, the minimum was none. Of those crabs that were recaptured within one month of liberty, the average distance travelled per day was approximately one meter. The

crabs captured more than once moved both landward and seaward. There was no indication of any seasonal trend in direction of movement.

Twelve crabs were found dead. Seven of these crabs died within one month of tagging. One was soft-shelled when tagged, and may have been injured. Three dead crabs were found after three, five, nine, and 11 months, respectively, but crab #7 was found dead over 700 days after it was tagged. All of the dead crabs, and three tags that came loose from tagged crabs, were found only a short distance from the study areas, usually on the narrow beach near the cliffs above the tide pools. Although intertidal areas of the Reserve are heavily visited by classes, guided tours, and the general public throughout the year, no tags or tagged crabs were found or reported elsewhere in the Refuge during the period of study.

Discussion

As in our previous study, we found no evidence of long-term defence of a fixed territory in rock crabs. Carroll (1982), in a study of subtidal rock crabs in Diablo Canyon, reported that rock crabs could travel distances of up to 7 kilometers. Because of high surf, we were unable to monitor movements of crabs into subtidal regions. Crabs in our study areas moved up to 35.7 m within or between transects. Those that were recaptured seemed to stay in a channel in a small area (perhaps as small as 500 m²) for as much as a month, and then leave permanently.

Of the 317 crabs that were not observed again after tagging, some undoubtedly died and others lost their tags. Carroll (1982) estimated tag loss at 14% in his study at Diablo Canyon. The crabs that were not recaptured at the Refuge probably moved to subtidal areas or traversed the subtidal regions in moving to other areas of the intertidal zone. The channels give easy access to subtidal areas nearby, where surf, a rugged rocky bottom and generally poor visibility (approximately 1 m) made it difficult to observe crabs. We have observed rock crabs running in synchrony with the surge in the channels at high tide, which suggests that movement takes place when the crabs are submerged. Indeed, the crabs only moved at low tide when greatly disturbed.

During low tide, the crabs usually take shelter in cracks and under larger rocks in the channels. Shelter apparently is very important to rock crabs during the few unusually hot days that occur along this coast every year. We have recorded water temperatures of up to 20°C in the intertidal zone for more than an hour during "minus" tides. MacKay (1943) reported that species of *Cancer* are restricted to waters with a mean annual temperature of 23.9°C or less. Rock crabs which remain in the intertidal zone, therefore, may be exposed to temperatures near the limits of their tolerance for more than an hour. On 7–9 April 1989, when the air temperature reached 32°C and water temperature reached over 20°, six dead rock crabs (not tagged) were found in tidepools in the mid-tide zone (2.5 to 0.0 foot tide level). Rock crabs seem to prefer the shelter of a deep crevice or a hiding place under a large rock.

Having studied crabs in the channels previously, we are reasonably certain that we located all of the larger rock crabs present per study date and that an absence of a tagged crab was not due to it being overlooked by an observer. (Although rock crabs have been observed to bury themselves in the sand, the sand layer in the channels is shallow and the crevices are not so deep that crabs cannot be seen). Recapture rates per individual declined sharply with time, with only nine crabs

Table 4. Recaptured crabs.

Numbers and sex of crabs recaptured per month					
November 1987	—	—	September	—	—
December	2M	—	October	1M	3F
January 1988	7M	2F	November	1M	2F
February	4M	3F	December	1M	3F
March	3M	3F	January 1989	1M	6F
April	1M	1F	February	3M	5F
May	2M	1F	March	2M	2F
June	4M	6F	June	—	2F
July	1M	2F			
August	—	1F			

Crabs recaptured after 2 months or more

Crab number	Date tagged	Date recovered	Interval in days
17	12/3/87	2/1/88	60
56	1/6/88	6/14/88	159
63	1/18/88	5/17/88	119
92	2/1/88	6/15/88	134
152	3/31/88	6/1/88	62
216	6/14/88	3/21/89	280
274	8/29/88	3/5/89	188
366	1/3/89	6/20/89	198
384	2/6/89	6/20/89	134

Crabs recaptured more than once

Crab number	Date tagged	Date recovered
130	3/9/88	3/14/88, 3/15/88
152	3/31/88	6/1/88, 6/14/88
298	10/11/88	10/27/88, 11/6/88
300	10/11/88	10/25/88, 10/27/88, 11/9/88, 11/10/88
340	12/7/88	12/19/88, 1/3/89, 1/19/89, 2/14/89
350	12/19/88	2/14/89, 2/21/89, 3/13/89
384	2/6/89	6/20/89, 7/4/89

(2%) recaptured after two months. Movement of new crabs into the transects is no doubt important in affecting recapture rates because nearly every new search of the transects revealed a different crab inhabiting a favored sheltering location under a rock or in a crevice. This apparent movement along with the low recapture rate prevents estimation of the local population size.

Why the sex ratio was skewed is unknown. Carroll (1982) reported that males generally outnumbered females subtidally at Diablo Canyon except during fall. He speculated that warmer temperatures may stimulate female crabs to move inshore. Our finding that female crabs were more common in intertidal areas during spring and summer seems to contradict Carroll's idea. Juvenile crabs often are found in the intertidal channels, where they constitute about half of the total number of crabs encountered (Breen and Wicksten 1988).

Based on the injuries and encrustation we observed as well as the lack of evidence

of molting or regeneration, we suspect that most of the rock crabs we tagged were full adults at or near their maximum size. Garth and Abbott (1980) reported that adult males of the species grew to 118 mm in carapace width and females to 78 mm. *Cancer antennarius* may slow their molting rate or stop molting on reaching sexual maturity, as is reported in *C. magister* (Garth and Abbott 1980).

Injuries and missing appendages were common in the rock crabs. Predators at the Refuge capable of injuring these large crabs include giant octopus (*Octopus dofleini*), larger red crabs (*C. productus*), cabezon (*Scorpaenichthys marmoratus*), and rarely sea otters (*Enhydra lutris*). Crabs could lose appendages during fights with conspecifics. Injuries may be caused by mechanical damage by battering by rocks during heavy surf. Visitor traffic also can cause injuries: fishermen have been seen tearing off chelipeds for food, then releasing the crabs; and careless visitors may smash them by overturning rocks.

Data from this and our previous study give no indication of preferential seasonal movements in rock crabs. Most crabs were tagged in our third transect, "South Moss Beach." The Channel and Surf Grass site can be covered by sand during winter, rendering it unsuitable for habitat by crabs. We have not observed more than 50 crabs in all three channels per study date, which suggests that the crabs occur in low densities and are dispersed through the habitat. At low tide, the crabs are found repeatedly in the same cracks, under large rocks or in pools. The finding of nine crabs back in the study area after an absence of two months or more as well as dead tagged crabs on the beach after up to nearly two years suggests that at least some of the crabs do not move long distances over time.

Our observations suggest that the shelter offered by crevices and larger rocks during low tide is important to the crabs. Such shelter also could be critical during winter storms—intertidal animals often are crushed or cast ashore during winter, when waves of 3 m or more sweep across the tidal flats and channels.

Acknowledgment

We thank Beth Arndt, graduate student at San Francisco State University, for her enthusiastic assistance.

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Accepted for publication 31 October 1989.

Status and Management of Shoshone Pupfish, *Cyprinodon nevadensis shoshone* (Cyprinodontidae), at Shoshone Spring, Inyo County, California

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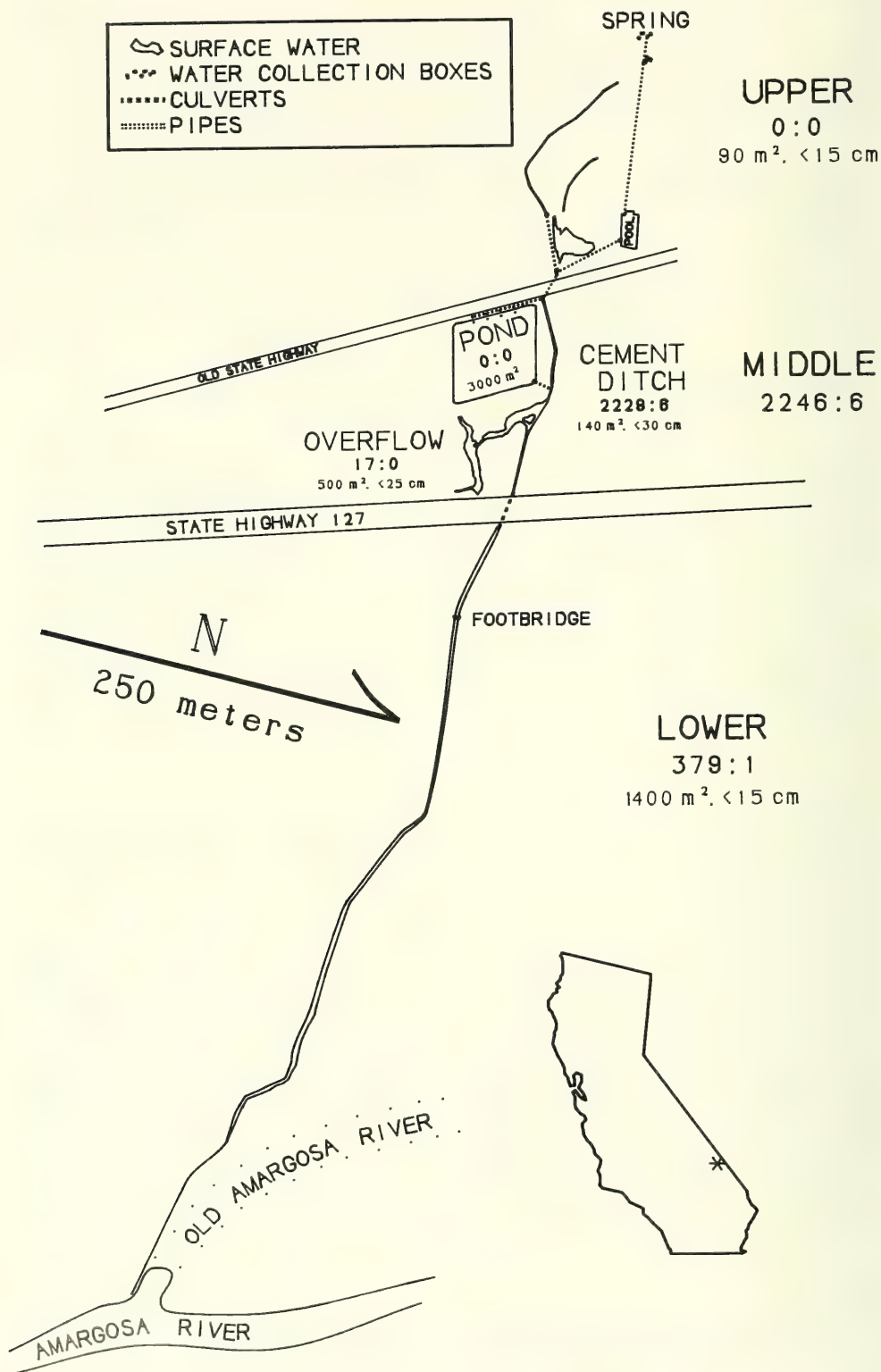
Abstract. — Shoshone pupfish (*Cyprinodon nevadensis shoshone* Miller), previously considered extinct, were rediscovered in 1986 from the outflow of Shoshone Spring. Plans to expand use of the water supply prompted us to map Shoshone Spring and determine habitat quality and distribution and abundance of pupfish. Pupfish in Shoshone Spring are threatened by habitat alteration, including reduced instream flow and pollution, and predation by and/or competition with introduced mosquitofish (*Gambusia affinis*). Because the continued existence of pupfish in Shoshone Spring seemed unlikely, we removed fish to establish a protected population to provide progeny for reintroduction.

Shoshone pupfish (*Cyprinodon nevadensis shoshone* Miller) were common in Shoshone Spring, Inyo County, California in 1938 (Miller 1948) but were considered extinct by November 1969 (Miller 1970). Fish closely resembling Shoshone pupfish were recently collected from the outflow of Shoshone Spring (Taylor et al. 1988). Rediscovery of pupfish and plans for further development of the spring area prompted us to gather more information on the fish and its habitat, information needed to develop a management plan to protect Shoshone pupfish. Our objectives were to map Shoshone Spring, determine the quality of the pupfish habitat, and determine the distribution and abundance of pupfish there. We surveyed Shoshone Spring on 15–18 April 1988. Because our observations differed from those of Taylor et al. (1988), we met Frances R. Taylor at Shoshone Spring on 25–26 May 1988 to compare the present habitat with her observations in July 1986 and to collect pupfish for propagation. We attempted to collect additional pupfish on 19 November 1988. This paper describes our findings and discusses the status and future management of Shoshone pupfish.

Methods

Mapping

We mapped Shoshone Spring (Fig. 1) using triangulation and 10 m transects, with compass readings on all distance measurements. Thick vegetation, primarily



mesquite (*Prosopis* sp.) and tamarisk (*Tamarix chinensis*), made triangulation over broad areas impossible, requiring us to map the spring in smaller sections and then align sections by common, cross-referenced landmarks. These data were then entered into a Generic CADD Level 3 (Generic Software, Inc., Redmond, Washington) drawing file to draw a scale map (Fig. 1) and estimate water surface areas of Shoshone Spring.

Fish Sampling

Shoshone Spring can be divided into three sections, with sections being delineated by Old State Highway and State Highway 127 (Fig. 1). We sampled fish in all three sections on 15–18 April, in the middle section on 26 May, and in the middle and lower sections on 19 November. We sampled available habitat using seines, dipnets, and minnow traps. Seining was restricted to areas of low vegetation density, and dipnetting and minnow traps were used in areas of high vegetation density. Although our sampling was qualitative in nature, we feel that we thoroughly sampled available fish habitat and were thus able to determine relative abundances of fishes in the system.

Results and Discussion

Habitat Description

Shoshone Spring is a highly altered habitat. Most of the spring water is captured by spring boxes and piped for local use. All channels are artificial, ditched as recently as 1985. Sections are separated by underground culverts or pipes that provide some barrier to fish movement. All wet areas were heavily overgrown with bulrush (*Scirpus* sp.) and cattails (*Typha* sp.).

The upper section (Fig. 1) receives minimal overflow (or leakage) from spring boxes. Pipes isolate the upper section from invasion by downstream fishes. The large puddle south of the pool (Fig. 1) was temporary.

Water diverted to the pool joins the spring water at a collection box and flows to the middle section (Fig. 1). Most of the water is piped into a large pond and the balance flows down the cement ditch. Water leaves the northeast corner of the pond and flows into the cement ditch (Fig. 1). Pipes provide a barrier to fish moving from ditch to pond. Vegetation and debris caused water to overflow the ditch, creating a marsh south of the cement ditch (Fig. 1). The ditch was cleared of vegetation after our April survey, causing the marsh to dry prior to our November survey. Water flowed continuously through the cement ditch ($3270 \text{ cm}^3 \cdot \text{sec}^{-1}$, 16 April 1988) but seemed to flow more rapidly as we seined out vegetation and debris. The cement ditch receives chlorinated water when the swimming pool is cleaned (as often as once a week [Susan Sorrells, personal communication]) and may dry when the pond is emptied and filled.

Water flows through a culvert to the lower section (Fig. 1). Because of its large diameter, this culvert has little effect on current velocity and probably provides

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Fig. 1. Scale map of Shoshone Spring on 17 April 1988. Ratios are numbers of mosquitofish to numbers of pupfish captured in the locations named above them. Numbers below ratios are area and greatest depth of locations named above ratios. Inset of California shows approximate location of Shoshone Spring.

Table 1. Location of capture, size, and sex of pupfish captured in Shoshone Spring on 16 April 1988.

Location	Sex	Size (mm)	
		Standard length	Total length
Middle	♀	>40	>46
Middle	♂	>40	>46
Middle	♂	54	62
Middle	♀	40	46
Middle	♂	43	48
Middle	♀	41	46
Lower	♀	51	58

only a moderate barrier to fish moving upstream. The lower section is more likely to dry than the cement ditch because it is downstream and has a sand substrate. The river's flood plain recently encompassed the lower end of the spring channel, suggesting that river and spring flows join at times of high water, possibly allowing fish movement between river and spring.

Water temperature at the spring source was 32°C and decreased downstream to 21.6° (air temperature 20.3°) on 16 April. Specific conductance ranged from 1458 to 1755 mhos·cm⁻³, pH from 6.7 to 7.4, and total dissolved solids from 1005 to 1207 mg·l⁻¹ on 17 April. Dissolved oxygen was 6.25 ppm at 30° at 1230 h on 16 April in the cement ditch.

Fish Distribution

We captured 2,625 mosquitofish (*Gambusia affinis*), but only 7 pupfish on 16–17 April. Mosquitofish were the most abundant fish in Shoshone Spring and have been abundant there as early as 1966 (Miller 1967; Selby 1977). In 1986, Taylor et al. (1988) found mosquitofish to be very abundant, but pupfish were also common (Frances R. Taylor, personal communication). Mosquitofish were much more abundant than pupfish in all areas in which we captured pupfish (Fig. 1). Although Miller (1948) collected pupfish in the upper section in 1938, we did not capture either species in this area, nor did Taylor et al. (1988) in 1986.

On 26 May, we captured 6 male and 3 female large adult pupfish and many more mosquitofish in the cement ditch. Six pupfish were captured before 0930 and 3 more just before 1730, but none were captured mid-day despite a comparable effort.

On 19 November, we captured one large female pupfish from the lower section along with numerous mosquitofish and observed 359 dead mosquitofish and one dead pupfish (male, 52 mm TL) in the cement ditch. The ditch water had a chlorine-like odor, suggesting that cleaning of the upstream pool might have been a causal factor. We were subsequently informed that the pool had been drained on 17 November and the sides sprayed with Purex® bleach to remove algae (Susan Sorrells, personal communication). The chemical was washed into the cement ditch and likely caused the mortality. An approximately equal number of live mosquitofish were observed in the ditch on 19 November, indicating that the kill was incomplete or that fish reinvaded the ditch from downstream sections that did not suffer mortalities.

Although recent surveys of Shoshone Spring found a wide size range of pupfish and therefore, presumably, ages (Frances R. Taylor, personal communication, Jack E. Williams, personal observation), we found only large adults (Table 1). A decline in pupfish abundance and a shift from a mixed size (age) structure to one of few large (older) fish suggests that we found only remnants of the population observed by Taylor et al. (1988) in 1986.

Minckley (1969) observed a population of Gila topminnows (*Poeciliopsis occidentalis*) as it was reduced from a large population with a mixed size structure to a population of a few old females by interactions with mosquitofish. A similar interaction between pupfish and mosquitofish in Shoshone Spring could explain reductions in pupfish numbers. Schoenherr (1981) presented evidence that mosquitofish eliminate topminnows by predation on fry and by reducing survivorship of adult females and numerous authors have suggested mosquitofish decimate pupfish populations (Deacon and Minckley 1974; Evermann and Clark 1931; Fisk 1972; Selby 1977; Soltz and Naiman 1978).

Habitat Assessment and Improvement

The present quality of pupfish habitat within Shoshone Spring system is low, and permanence of that which remains is questionable. The upper section relies on overflow or leakage from spring boxes for water, making this section unsuitable as a refuge. Absence of fish in this area attests to its poor quality. For the upper section to be used as a refuge, water would have to be supplied directly from the spring boxes to ensure permanent flow. Re-establishment of a spring pool (as in Miller 1948) may help ensure future suitability of the habitat as a refuge.

The middle and lower sections suffer from impermanence, especially in the overflow area, risk of chlorine pollution, and mosquitofish presence. Only the ditch holds promise as a refuge for pupfish but this area must be protected from chemical pollutants, trash, overgrowth, mosquitofish, and water diversion.

Attempts to improve pupfish habitat at Shoshone Spring should consider early accounts and attempt to return it to its original condition. A related species, the Devils Hole pupfish (*C. diabolis*), attained larger size and changed morphology when held for several generations in an artificial refuge (Williams 1977). Because habitats in which species evolve act to mold and maintain unique features of species (Pister 1981), it is important to return Shoshone Spring to its original condition to maintain Shoshone pupfish.

Early accounts suggest water now diverted for local use once flowed from Shoshone Spring, creating extensive fish habitat (Miller 1948; Wales 1930). Miller (1948) visited Shoshone Spring in 1937 and described two pools in the upper section and a swiftly flowing channel extending to below Old State Highway where flow slowed to form a 0.9 to 1.8 m wide, <60 cm deep creek 1.2 km long. Using Miller's (1948) data on length and width of pupfish habitat at Shoshone Spring, we estimate 1100 to 2200 m² of habitat in 1937. Summing areas inhabited by pupfish in our study, we estimate 740 m² of habitat on 17 April 1988. Comparing these figures, we calculate a 33 to 66% reduction in pupfish habitat at Shoshone Spring. Furthermore, this estimate only considers habitat area and not volume or flow. Because water depths were shallow over most of the area we measured and our maximum depth (<30 cm) was half of that reported by Miller (1948), it is likely that reduction in habitat volume has been much greater than the reduction

in habitat area. Selby (1977) and Taylor et al. (1988) also described greater water surface area and flow rates than we observed. Any plan to improve Shoshone Spring should include increasing available pupfish habitat, but will need to balance pupfish protection and local water use.

Early accounts also described the pupfish habitat as being bordered by cattails and mesquite (Miller 1948; Wales 1930). Tamarisk is now the dominant riparian vegetation shading large portions of the spring channel. Tamarisk may alter water and nutrient balance in the spring channel. Plans to improve Shoshone Spring should consider removing tamarisk.

Mosquitofish were introduced to Shoshone Spring sometime after 1938 (Miller 1948) and before 1967 (Miller 1967). Selby (1977) argued for mosquitofish eradication to improve Shoshone Spring's potential as pupfish habitat. On both of our visits, we removed all of the mosquitofish we captured. Before a secure pupfish population can be reestablished in Shoshone Spring, mosquitofish must be eliminated.

Because of the low number of pupfish in the system and the tenuous nature of all habitats, we decided to remove as many pupfish as possible to establish a captive breeding population for potential reintroduction to the spring. On 26 May, we removed six male and three female pupfish from the cement ditch and on 19 November, we removed one additional female from the lower section. These fish are now being held at the University of California, Davis. In addition to propagating pupfish, action must be taken to restore pupfish habitat before reintroducing them.

Fish Origin

Taylor et al. (1988) presented three hypotheses which might explain "reappearance" of pupfish in Shoshone Spring: invasion, introduction, or non-detection (fish were there, but at very low abundance, and escaped detection). They argued that a closer resemblance of rediscovered fish to Shoshone pupfish than to Amargosa pupfish (*C. n. amargosae*, the nearest related species) lends support only to the non-detection hypothesis.

Several factors have led us to question the non-detection hypothesis, and to suggest that the invasion and introduction hypotheses are still viable alternatives. First, Amargosa River and Shoshone Spring flows join at times of high water. Second, pupfish in the spring system would have been missed during several surveys (Miller 1967; Selby 1977). Even though pupfish numbers were extremely low during our visit, we were able to document their presence. Third, fish collected by Taylor et al. (1988) did not match Shoshone pupfish exactly and they suggest that differences resulted from a genetic bottleneck. Differences could also be due to Shoshone pupfish changing morphology while they inhabited the river prior to re-invasion (possibly due to the physical environment or interbreeding with Amargosa pupfish), or Amargosa pupfish coming to resemble Shoshone pupfish while isolated in Shoshone Spring. While the involvement of Amargosa pupfish in the reappearance of Shoshone pupfish seems unlikely, such an occurrence would have important implications for pupfish management and evolutionary and conservation biology. More research is needed to determine the status of pupfish in this area of the Amargosa River drainage. This information will be necessary for proper management of these fish and their threatened habitats.

Acknowledgments

Susan Sorrells of Shoshone Development, Inc. kindly provided background information, housing, and permission to conduct our surveys. Betsy C. Bolster and Mignon P. Shumway of the California Department of Fish and Game, Eric Wikramanayake of the University of California at Davis, and Todd N. Persons of Oregon State University assisted in field collections. Frances R. Taylor provided a first hand account of habitat conditions that prevailed during her 1986 survey (Taylor et al. 1988). Drs. Joseph J. Cech, Jr., Peter B. Moyle and Allen W. Knight of the University of California, Davis loaned equipment.

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Accepted for publication 25 April 1989.

Comparative Photosynthesis, Water Relations, and Nutrient Status of Burned, Unburned, and Clipped *Rhus laurina* after Chaparral Wildfire

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¹Published posthumously. Mr. Roy Stoddard was lost at sea January 26, 1989

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Abstract.—We compared photosynthesis, water relations, and leaf nitrogen contents among burned, clipped, and mature shrubs of *Rhus laurina* after a wildfire in the Santa Monica Mountains of southern California. Within the first year after fire, photosynthesis, stomatal conductance, and nitrogen contents for individual leaves were elevated for burned and clipped plants as compared to mature shrubs. Except for foliar nitrogen contents, these differences disappeared within 14 months after fire. Within 17 months after fire, resprouts of burned and clipped shrubs had a total leaf area and total leaf nitrogen content about twice that of mature plants. These results indicate that during the first year after fire, enhanced photosynthetic performance of individual leaves contributes to the rapid recovery of shoot tissue—in succeeding years, enhanced total leaf area and total canopy photosynthesis continue the recovery process.

The chaparral vegetation of California is primarily comprised of evergreen, sclerophyllous shrubs that are resilient to periodic disturbance by wildfire (Hanes 1971; Keeley 1986). One of the most common and successful modes of recovery after wildfire is by vegetative sprouting from a root crown (James 1984; DeSouza et al. 1986). Wells (1969) pointed out some time ago that all 25 genera of chaparral shrubs in California have a crown-sprouting trait whereas only 2 genera contain species that are non-sprouters. It appears that crown-sprouting is important for the post-fire recovery of chaparral vegetation because seeds of some species are killed by fire (obligate resprouters, Keeley 1986) and post-fire seedlings generally suffer high mortality due to competition with annual herbs and grasses (Schultz et al. 1955), herbivory (Mills 1983), and water stress during the first summer drought after fire (Kummerow et al. 1985; Frazer and Davis 1988; Thomas and Davis 1989).

Available data indicate that vegetative sprouting after fire provides a number of competitive advantages over seedling recruitment for chaparral shrubs: 1) prefire position is maintained, 2) shoot elongation is rapid and is initiated soon after fire, 3) reproductive maturity is quickly reached, and 4) competition for light, moisture, and nutrients is enhanced (Keeley and Zedler 1978). Obvious disadvantages of vegetative sprouting are the lack of genetic recombination with each post-fire generation and the inability to invade new microsites (Wells 1969).

The mechanism for the rapid recovery of chaparral resprouts after fire is not clearly understood. Indirect evidence indicates that carbohydrates and inorganic nutrient reserves in the root and root crown are mobilized soon after fire, releasing

bud dormancy in the root crown, and initiating the rapid regeneration of new stems and leaves (Adams and Radosevich 1978; Rundel 1981). It is probable that carbohydrate reserves in the root crown also maintain the respiratory needs and thus activity of an extensive, below ground root system (Parsons et al. 1981; DeSouza et al. 1986). The survival of a large water uptake system (root) with little surface area for water loss (leaves) suggest a luxurious supply of moisture to shoot tissue during the first growing season after fire. Thus water status and turgor potentials remain favorable for continued shoot elongation of resprouts even during dry summer months (DeSouza et al. 1986; Saruwatari and Davis 1989). In addition to improving the water status of resprout tissue, retention of a large active root system after shoot removal may also facilitate the rapid uptake of inorganic nutrients from post-fire soils (Rundel and Parsons 1980). Elevated water and nutrient status probably contribute to the high stomatal conductance and photosynthetic rates observed for resprouts during the first growing season after fire (Radosevich and Conard 1980; Oechel and Hastings 1983; DeSouza et al. 1986; Hart and Radosevich 1987; Hastings et al. 1989).

Here we examine the resprouting process of a common member of coastal chaparral of southern California: *Rhus laurina* Nutt. (laurel sumac). Our objectives were to compare the water status, leaf nitrogen content, and photosynthetic performance of unburned shrubs to resprouts of burned and clipped individuals. We predicted that relative to unburned shrubs, 1) resprouts of burned and clipped shrubs would have higher water status and leaf nitrogen contents, 2) resprouts of burned and clipped shrubs would initially have enhanced photosynthetic rates, and 3) eventually differences between treatments would disappear as total leaf area returned to pretreatment values. Furthermore, we reasoned that clipped shrubs would have lower leaf nitrogen contents and photosynthetic rates than burned shrubs because the soil beneath clipped shrubs would not receive nutrient-rich ash deposited by the fire.

Study Site

Our study site is located 1 km east of the Malibu campus of Pepperdine University (34°02'30"N, 113°41'44"W), on a SW facing slope (mean incline of 10°) of the Santa Monica Mountains, at an elevation of 150 m. The prefire stand consisted of mixed chaparral shrubs dominated by *Ceanothus megacarpus* Nutt., and *Rhus laurina* Nutt. (Frazer and Davis 1988). Nomenclature follows Munz (1974). The study site had not burned since September 1970 (Los Angeles County Fire Department).

Our study site was burned in a 0.6 ha wildfire on 21 April 1984. During the fire, fire fighters hand-cleared a 5 m wide fire-break around the perimeter of the burn site. As a result, burned shrubs were surrounded by a 5 m wide strip of clipped shrubs and outside this strip was an extensive stand of unburned plants. This facilitated a comparison of three treatments—burned, clipped, and unburned shrubs. We were careful to select clipped and unburned shrubs that were uphill of the burned treatment. Therefore, it was unlikely that nutrients leached from burned soils during fall and winter rains were received by clipped and unburned individuals.

We chose *R. laurina* as our experimental subject because previous data indicated that this species had a prominent root crown, deep roots, and virtually 100%

resprouting success after wildfire (DeSouza et al. 1986; Frazer and Davis 1988; Thomas and Davis 1989).

On 14 October 1985, a second wildfire burned a large area surrounding our study site. Once the fire reached our previously established fire-break, it depleted its fuel and extinguished itself. However, the clipped shrubs in the fire-break were heat damaged and measurements on these plants were discontinued. A number of mature individuals were undamaged by the second fire, permitting us to continue our original comparison between burned and unburned treatments.

Methods

Soil Water Potential and Soil Temperature

An electric drill and masonry bit were used to drill one hole beneath the unburned shrubs, one beneath post-fire resprouting shrubs, and one in an open area of the burn site, devoid of resprouts. We did not drill a hole beneath clipped shrubs. Each hole was 25 mm in diameter and 2 m deep. Soil psychrometers (model PCT-55-30, Wescor Inc., Logan, Utah) were calibrated at 4 points using standard NaCl solutions. We installed 8 psychrometers in each hole at 0.25 m intervals in depth. Holes were back filled with original soil. A dew point microvoltmeter (model HR-33T, Wescor Inc.) was used to measure soil temperatures and soil water potentials, with these psychrometers, once every two weeks between May 1985 and January 1986, following the precautions and procedures given by Weibe et al. (1977) and Weibe and Brown (1979). We measured soil temperature and water potential at dawn because we wanted to standardize the time of measurement and because we found thermal gradients, especially near the soil surface, to be minimal at this time of day. Soil water potential values were not accepted if zero-offset readings exceeded 3.0 μV .

Predawn Water Potentials

We measured leaf water potentials (Scholander et al. 1965) every two to three weeks between May 1985 and January 1986. Readings were taken on 2 leaves from each of 3 plants in each treatment. To prevent phloem exudate from interfering with the measurement of true xylem water potentials, phloem was removed from petioles, with electrical wire strippers, just prior to the insertion of each leaf in the pressure chamber. Periodic measurements of predawn water potentials were also taken on *C. megacarpus* in the mature, unburned stand to aid our assessment of the relationship between plant water status and soil water potential. Thomas and Davis (1989) have found that maximum rooting depth of *C. megacarpus* does not exceed 2 m whereas roots of *R. laurina* extend much deeper than 5 m. We reasoned that a comparison of predawn water potential between *C. megacarpus* and *R. laurina* growing together would indicate the soil moisture environment of shallow roots, versus deep roots in our system. Furthermore, the theory of hydraulic lift (Richards and Caldwell 1987) suggests that deep rooted shrubs should loose moisture to shallow, dry regions of the soil overnight. If this was the case in our system, we predicted that the soil moisture profile beneath unburned *R. laurina* in the presence of *C. megacarpus* would be much different than beneath *R. laurina* resprouts devoid of *C. megacarpus* (*C. megacarpus* is a non-sprouter

after fire and thus vegetative sprouts of this species were absent in the burned and clipped treatments).

Pressure-Volume Curves

In order to compare the tissue water relations of the burned, clipped, and unburned shrubs, we used a modified pressure volume technique that has been fully described elsewhere (Davis and Mooney 1986a; DeSouza et al. 1986). In June of 1985, one branch from each of four burned, four clipped, and four unburned plants was cut under water, covered with a plastic bag, and allowed to rehydrate overnight in complete darkness. The next morning, one fully expanded leaf was removed from each branch and used to determine the osmotic potential at saturation ($\Psi_{s(sat)}$), osmotic potential at the turgor loss point ($\Psi_{s(tlp)}$), relative water content where turgor is lost (RWC_{up}), bulk modulus of elasticity (ϵ), bound water of the bulk tissue (B), and the saturation weight/dry weight ratio (SW/DW).

Diurnal Leaf Conductance and Photosynthesis

Diurnal photosynthesis and leaf conductance to water vapor diffusion were measured using a portable photosynthesis system (model LI-6000, Li-Cor Inc., Lincoln, NE). Measurements were taken on 3 fully illuminated and enlarged leaves of each plant for 3 plants from each treatment. In July 1984, initial readings were taken on burned and unburned shrubs only. The following season, 1985, measurements were made on all three treatments, burned, clipped, and unburned, once each month, from May to August 1985.

Nitrogen Content of Leaf and Stem Tissue

After each diurnal measurement of photosynthesis, experimental leaves were harvested and brought back to the laboratory for nitrogen determinations ($N = 9$ for each treatment). The area of each leaf was calculated using a digitizer (Hipad, Houston Instrument, Austin, Texas). Leaves were then oven dried at 80°C for at least 48 hours, weighed to the nearest 0.1 mg with an analytical balance, and used to measure nitrogen content (% dry weight) by the micro-Kjeldahl digestion and titration method (Nutritional Analysis Lab., Range Science Dept., Colorado State Univ., Fort Collins, Colorado). Leaf specific weight and total leaf nitrogen per area of the leaf were calculated. Stem tissue was also dried, weighed, and subjected to nitrogen analysis in September 1985.

Total Shoot Biomass and Leaf Area

On 28 September 1985, we estimated the average leaf area and shoot biomass of unburned, clipped, and burned shrubs by the following method. First, we randomly selected 3 individuals from each treatment and counted the number of main branches per plant. Second, we randomly selected three main branches from each shrub and calculated the total leaf area per branch by taking the product of length and width of each leaf and multiplying by a constant (0.761) derived from a regression of leaf area versus leaf dimension ($r^2 = 0.97$, $N = 39$). Finally, stem and leaf tissue from each branch were separated, oven dried at 80°C for at least 48 hours, and weighed to the nearest 1 mg. These mean values of leaf area and

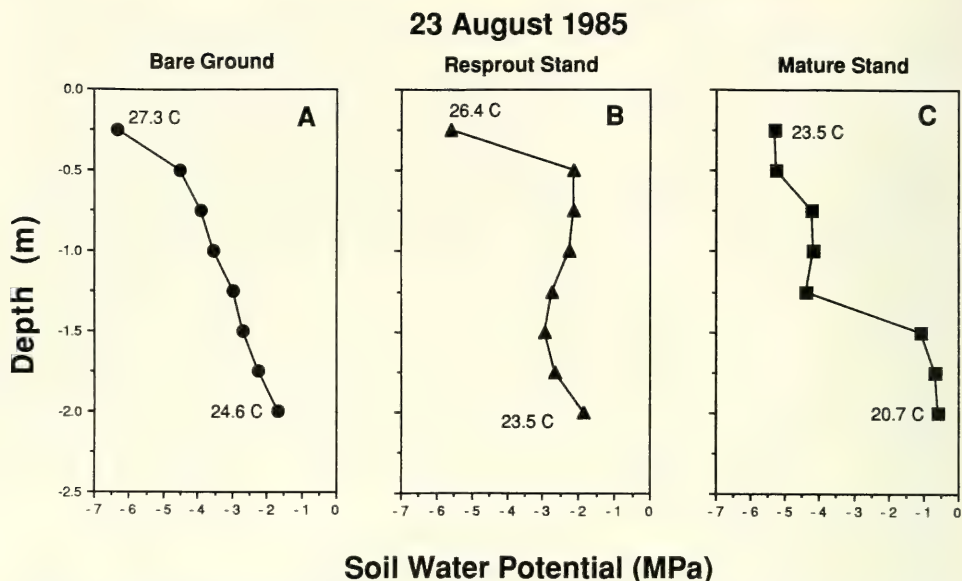


Fig. 1. A–C. Soil water potentials and corresponding temperatures at 0.1 m and 2.0 m depths for (A) bare ground, (B) resprout, and (C) mature sites on 23 August 1985.

dry weights per branch were then multiplied times the average number of branches per plant in each treatment to calculate total shoot biomass and leaf area.

Statistical Analysis

Mean values of predawn water potential, nitrogen content, tissue water parameters, and shoot biomass were compared by either a Student's *t*-test, or a one way ANOVA depending on the number of groups involved. Mean values of diurnal photosynthesis, leaf conductance, and leaf water potentials were compared by two way ANOVA followed by a Scheffe's multiple range test. All means were compared at the 0.05 level of significance (Sokal and Rohlf 1981).

Results

Soil Water Potential and Soil Temperature

Soil water potentials continually decreased at the bare ground, resprout, and mature sites as the summer drought progressed (data not shown). In August 1985, the bare ground site, presumably devoid of active root systems, had an almost linear decline in water potential with depth whereas the other two sites varied in their relation between water potential and depth (Fig. 1). These patterns were persistent throughout the summer drought period (data not shown).

During the summer, the difference in soil temperature between a depth of 0.25 m and 2.0 m was about 3°C at the bare ground, resprout, and mature sites. At the peak of the drought, in August 1985, soil temperatures at a depth of 0.25 m were higher at the bare ground and resprout sites than at the mature stand, probably because of shading provided by the foliage of mature shrubs (Fig. 1). The lowest temperature measured (20.7°C) was coincident with the highest soil water potential (−0.6 MPa), at a depth of 2.0 m in the mature stand.

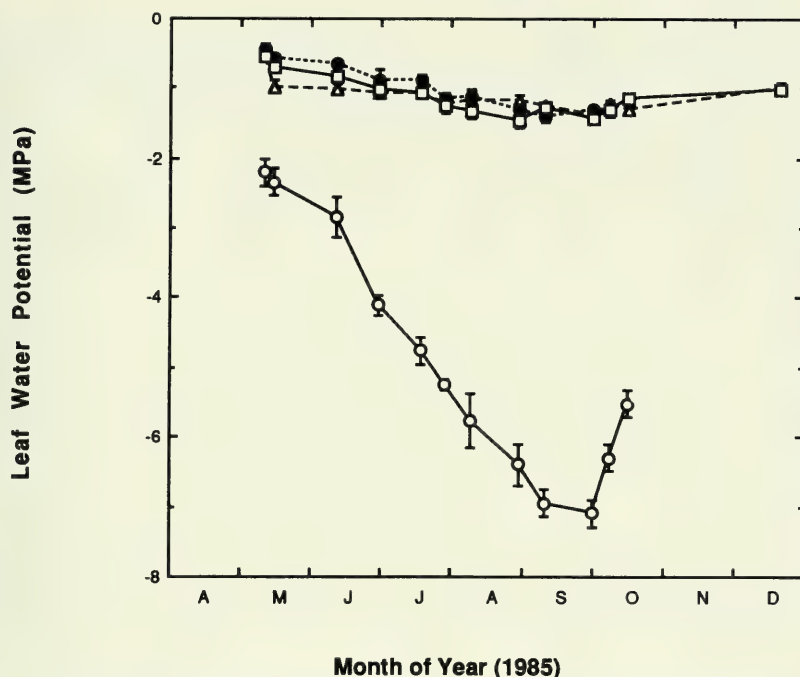


Fig. 2. Seasonal change in predawn water potentials from May to December 1985 for mature *Ceanothus megacarpus* (○), and three treatments of *Rhus laurina*—mature (□), burned (△), and clipped (●).

Predawn Water Potentials

There was a gradual decrease in predawn water potentials for burned, clipped, and unburned shrubs of *R. laurina* during the summer drought of 1985 (Fig. 2). Water potentials were similar between treatments and never reached values lower than -2 MPa. In contrast, mature shrubs of *Ceanothus megacarpus* came under severe water stress during summer months and reached predawn water potentials of -7 MPa by September 1985.

Pressure-Volume Curves

Tissue water relations between burned, clipped, and unburned shrubs of *R. laurina* were similar in June 1985 (Table 1). The only significant difference among treatments was that unburned shrubs had more rigid tissues than clipped shrubs (lower bulk modulus of elasticity). The osmotic potentials where bulk leaf tissues lost turgor varied between -2.2 and -2.4 MPa, values lower than predawn water potentials (Fig. 2) and minimum diurnal water potentials (Fig. 3C, F, I).

Diurnal Leaf Conductance and Photosynthesis

Photosynthetic rates measured 3 months after the fire of April 1984 were significantly higher at 3 points of the diurnal for the burned plants when compared to the unburned controls (Fig. 3A). Similarly, the burned treatment showed elevated conductance rates and water potential readings throughout the day in com-

Table 1. Mean values of osmotic potential at saturation ($\Psi_{s(\text{sat})}$), osmotic potential at turgor loss point ($\Psi_{s(\text{tlp})}$), bulk modulus of elasticity (ϵ), bound water (B), relative water content at the turgor loss point (RWC_{tlp}), and saturation weight/dry weight ratio (SW/DW) for leaves of burned, clipped, and mature *Rhus laurina* shrubs in June 1985. Mean values were compared by one way ANOVA followed by a Scheffé's multiple range test.

	Burned	Clipped	Mature
$\Psi_{s(\text{sat})}$ (MPa)	-1.6 (0.06)	-1.7 (0.08)	-1.8 (0.09)
$\Psi_{s(\text{tlp})}$ (MPa)	-2.2 (0.02)	-2.3 (0.09)	-2.4 (0.08)
ϵ (MPa)	9.2 (2.69)	12.3 (1.73)	6.8 ^c (0.54)
B (%)	36.1 (2.1)	41.7 (3.6)	35.9 (7.4)
RWC_{tlp} (%)	84.3 (1.5)	86.9 (0.6)	83.4 (0.9)
SW/DW	2.8 (0.03)	2.7 (0.15)	2.6 (0.04)

¹ Values in parentheses represent 1 S.E., N = 4.

² Letters in superscript represent significant differences at the 0.05 level from; b = burned, c = clipped, and m = mature plants.

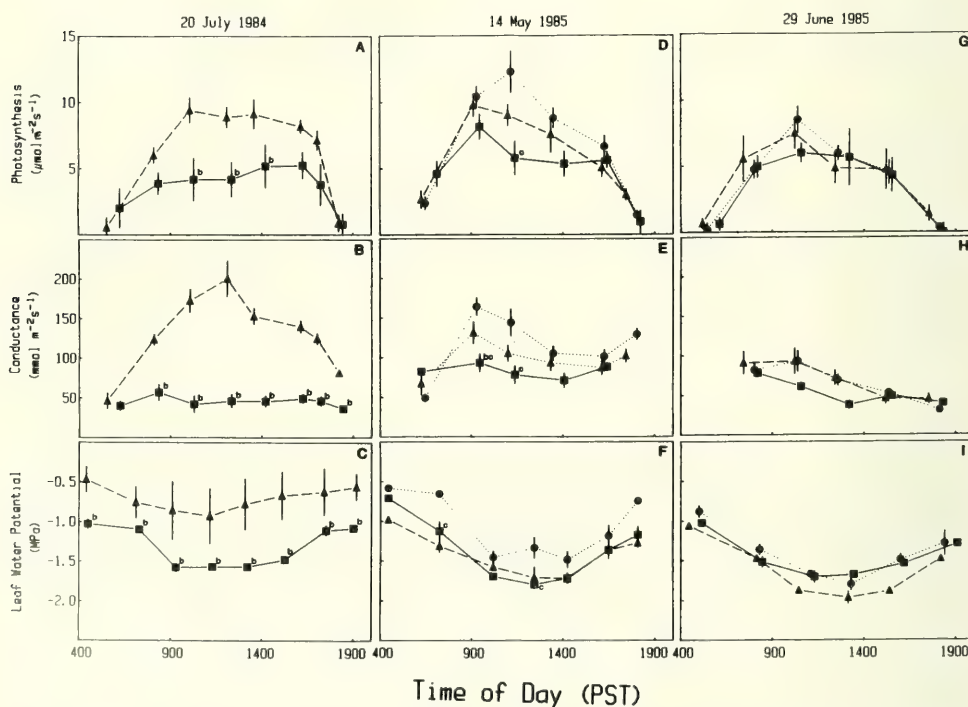


Fig. 3. Diurnal patterns of leaf photosynthesis (A, D, G), leaf conductance to water vapor diffusion (B, E, H), and leaf water potentials (C, F, I) for *Rhus laurina* following the wildfire of 21 April 1984. Treatments include mature (■), burned (▲), and clipped (●) individuals. Superscript letters indicate significant difference ($P < 0.05$) at that point from the mature shrubs where b = burned treatment and c = clipped treatment.

Table 2. Comparison of leaf nitrogen contents for burned, clipped, and mature shrubs expressed as a percentage (grams nitrogen/grams dry weight of leaf tissue) and as mass per unit area (grams nitrogen/area of leaf tissue). Mean values were compared either by Students t-test or one way ANOVA followed by a Scheffe's multiple range test depending on whether two or three treatments were involved.

Date	% Leaf nitrogen (g/g)			Area leaf nitrogen (g/m ²)		
	Burned	Clipped	Mature	Burned	Clipped	Mature
July '84	1.09 (0.01)	—	0.72 ^b (0.03)	—	—	—
May '85	1.49 (0.09)	1.66 (0.09)	1.18 ^{b,c} (0.05)	2.56 (0.02)	2.58 (0.09)	2.20 ^{b,c} (0.07)
June '85	1.12 (0.05)	1.08 (0.03)	0.95 ^{b,c} (0.06)	2.49 (0.17)	2.37 (0.11)	2.12 ^b (0.12)
July '85	1.12 (0.10)	0.98 (0.06)	0.95 ^b (0.11)	3.19 (0.12)	2.88 (0.11)	2.57 (0.24)
August '85	1.18 (0.04)	1.18 (0.05)	0.92 ^{b,c} (0.03)	2.90 (0.20)	2.82 (0.26)	2.23 (0.15)
October '85	1.03 (0.03)	—	0.90 ^b (0.03)	2.75 (0.07)	—	2.01 ^b (0.10)
January '86	1.94 (0.14)	—	1.34 ^b (0.16)	2.84 (0.07)	—	2.45 ^b (0.07)
July '86	1.17 (0.06)	—	1.04 (0.02)	2.57 (0.10)	—	2.09 (0.05)

¹ Values in parentheses represent 1 S.E., N = 9.

² Letters in superscript represent significant differences from mature shrubs: b = burned, and c = clipped, at a 0.05 confidence level.

parison to the mature treatment (Fig. 3B, C). Readings were not taken on the clipped treatment at this time.

Measurements taken on the same plants in May of the next year, and on the additional clipped treatment, were similar in that both the burned and hand cleared shrubs had slightly elevated photosynthetic rates over mature shrubs (Fig. 3D). However, these differences were not large, and only the clipped treatment was significantly higher in photosynthetic rate than mature plants at one point in the day. Conductance rates were significantly greater for both burned and clipped treatments than mature plants during early morning hours (Fig. 3E). Water potentials of the clipped plants were significantly higher than the mature plants at two points during the day, while the burned plants were not significantly different from mature plants at any time (Fig. 3F).

The physiological differences found in May were not observed in June. There were no significant differences in photosynthetic rates, conductance rates, or the water potentials at any hour of the day between any of the groups (Fig. 3G-I). Monthly diurnal measurements indicated no significant difference between groups throughout the remainder of the summer and fall (data not shown).

Nitrogen Content of Leaf Tissue

Percent leaf nitrogen for burned shrubs was elevated over mature plants on every month measured for two years following fire (Table 2). Leaf nitrogen expressed on an area basis was also elevated over mature plants on all months except

Table 3. Biomass and nitrogen distribution between leaf and stem tissues of burned, clipped and mature *Rhus laurina* shrubs on 28 September 1985. Mean values were compared by one way ANOVA followed by Scheffe's multiple range test.

	Biomass (g)			Nitrogen (g)		
	Burned	Clipped	Mature	Burned	Clipped	Mature
Leaf	881 (266)	835 (95)	467 ^{b,c} (53)	10.4 (3.1)	9.9 (1.1)	4.3 ^{b,c} (0.5)
Stem	281 (985)	396 (51)	1596 ^{b,c} (181)	1.6 (0.5)	1.9 (0.3)	6.5 ^{b,c} (0.7)
Total	1163 (351)	1232 (146)	2063 ^{b,c} (234)	12.0 (3.6)	11.8 (1.4)	10.4 (1.2)

¹ Values in parentheses represent 1 S.E., N = 3.

² Letters in superscript indicate significant differences from mature shrubs at a 0.05 confidence level: b = burned, and c = clipped treatments.

July and August 1985 (Table 2). Clipped shrubs had a higher percentage of leaf nitrogen than mature plants on all months measured except July 1985. However, when leaf nitrogen contents of clipped shrubs were expressed on an area basis, significant differences between treatments were observed only in May 1985 (Table 2).

Total Shoot Biomass, Nitrogen, and Leaf Area

Total leaf areas in September 1985 were significantly greater for both the burned and clipped treatments when compared to the unburned, mature plants. The burned treatment had an area of $7.4 \text{ m}^2 \pm 1.6$ (SE, N = 3), the clipped treatment $6.4 \text{ m}^2 \pm 1.2$, and the unburned treatment $2.7 \text{ m}^2 \pm 0.06$.

Most of the shoot biomass was in leaf tissue for both the burned and clipped treatments by September 1985 whereas mature shrubs had most of their shoot biomass in stem tissue (Table 3). Total shoot biomass was significantly lower in both resprout treatments as compared to mature shrubs, even after 17 months of postfire regrowth. Most of the total shoot nitrogen was located in the leaf tissues of resprouts, whereas most of the total shoot nitrogen was located in the stem tissue of mature plants (Table 3). Total shoot nitrogen was not significantly different among treatments.

Discussion

Water Relations

The water status of *R. laurina* resprouts were significantly higher than for mature shrubs during the first summer drought after fire but this difference disappeared by the second summer of regrowth (Fig. 3; Table 1). We suspect that this pattern was caused by the large root system of *R. laurina* initially supplying luxurious amounts of moisture to a diminutive shoot but as leaf areas returned to prefire values these differences disappeared.

There were large differences in soil moisture profiles that developed among bare ground, resprout, and mature sites by the second summer drought after fire (Fig. 1). Because the soil at our study site is a relatively deep and uniform deposit of

sandy loam, we suspect that this pattern was caused by differences in root activity. The bare ground site represented a soil moisture profile characteristic of a region devoid of deep roots. Only sparse numbers of herbaceous grasses and annuals with some seedlings of *C. megacarpus* and *R. laurina* were present. The seedlings did not have a rooting depth greater than 50 cm by August 1985 (Frazer and Davis 1988). Therefore, we assume that the decline in water potential with soil depth was primarily due to evapo-transpiration from the upper soil horizons (first 50 cm). In contrast to the bare zone, the mature site consisted of a dense stand of mature *R. laurina* and *C. megacarpus* shrubs that had very different rooting depths—greater than 5 m for *R. laurina* and less than 2 m for *C. megacarpus* (DeSouza et al. 1986; Thomas and Davis 1989; Davis and Mooney 1986a). Therefore, we suspect that the extremely low soil water potential in the first 1.5 m depth was due to the shallow root activity of *C. megacarpus* which had a predawn water potential near -7 MPa by the end of August 1985 (Fig. 2). In contrast, predawn water potentials for mature *R. laurina* growing adjacent to *C. megacarpus* were only about -1.5 MPa in August and corresponded to soil water potentials below 1.5 m (Fig. 2).

Most interesting were the relatively high soil water potentials at all depths below 0.5 m at the resprout site. This particular site had a dense cluster of 8 to 10 resprouting shrubs of *R. laurina*. We suspect that the deep roots of *R. laurina* were removing moisture from deep soil reserves but shallow roots were losing some of the water to shallow soil horizons, especially overnight. This interpretation needs additional verification but it is consistent with the patterns reported for *Artemisia tridentata* (Richards and Caldwell 1987) and *Prosopis tamarugo* (Mooney et al. 1980) under field conditions.

Diurnal Leaf Conductance and Photosynthesis

It appears that within three months after fire, there is a significant enhancement in photosynthesis, conductance, and water potential for burned *R. laurina* as compared to unburned shrubs (Fig. 3A–C). These results are consistent with those reported by DeSouza et al. 1986. However, unlike the results of DeSouza et al., the observed enhancement in our experimental system disappeared within 14 months after fire (Fig. 3G–I). The reason for this difference is not clear. Several factors may be involved, the most important of which is a lower availability of soil nutrients and moisture at our study site. The mean canopy height of mature shrubs at the DeSouza site was $4.1 \text{ m} \pm 0.32$ (SE, $N = 10$) whereas the mean canopy height of mature shrubs at our site was only $1.6 \text{ m} \pm 0.10$, suggesting very different resource availabilities for overall shoot construction.

Nitrogen Content of Leaf and Stem Tissues

The clipped plants at our study site were similar to burned plants, although the data are limited. At no time did we find significant differences in photosynthesis, conductance, leaf nitrogen, and water relations between burned and clipped treatments (Figs. 2, 3; Tables 1, 2). By September 1985, 17 months after wildfire, total leaf area, biomass, and nitrogen of shoots were almost identical between burned and clipped shrubs (Table 3).

Since we found no evidence that burned shrubs had a significant nutrient enhancement over clipped shrubs, we suspect that elevated values of leaf nitrogen were not a direct result of greater nitrogen availability and uptake from burned

soils. It is unlikely that the high foliar nitrogen observed for clipped shrubs came from the leachate of burned soils because the plants examined were uphill from the burn site. Furthermore, since the water potential between the soil surface and a depth of 1.5 m during summer months were lower than water potentials of plant tissues, it is improbable that shallow roots were actively taking up soil nitrogen from postfire char and ash deposited at the soil surface—yet leaf nitrogen remained elevated during summer months (Table 3). This implies that the elevated nitrogen in resprouts, whether burned or clipped, came from inorganic nutrients stored in the root.

Although there were no differences in total shoot nitrogen between burned, clipped, and mature shrubs, there was a dramatic difference in the distribution of nitrogen between leaf and stem compartments. Most of the mature shrub nitrogen was located in stems, whereas most resprout nitrogen was in leaves (Table 3). This difference in total nitrogen was primarily due to greater biomass of stem tissue in mature shrubs. Because leaf nitrogen has been shown to be directly proportional to photosynthetic rates in chaparral species (Field and Mooney 1983; Field et al. 1983), the increased nitrogen within leaves of the resprouts may enhance carbon gain to support new leaf construction. The increase in total leaf area would then lead to an overall increase in canopy photosynthesis as compared to mature plants, resulting in higher levels of whole plant carbon gain to support rapid growth rates. In addition, resprouts would not have the respiratory expense of sustaining a large stem biomass characteristic of unburned, mature plants. This may be one of the underlying mechanisms by which resprouts rapidly return to prefire conditions.

It is noteworthy that the total shoot nitrogen was the same among treatments by September 1985. This indicates that nitrogen may be limiting the construction of shoot tissues in our system. As shrubs are required to grow new and longer stems to compete for light, much of the available nitrogen becomes tied up in stem tissues and less becomes available for the construction of leaves. It may be that the nitrogen available for construction of shoots is not only limiting but fairly stable in our system throughout a fire cycle.

Acknowledgments

We are grateful to Marian Moyher, Peter Weldon, and Janet Davis for assistance with field equipment, to Dr. Kenneth Perrin for administrative support, and to Dr. Gary Tallman for helpful comments on a earlier version of the manuscript. This work was supported by grants from the John Stauffer Charitable Trust and the University Research Council of Pepperdine University. A version of this paper was submitted in partial fulfillment of the requirements of the Honors Biology program at Pepperdine University, Malibu, California.

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Accepted for publication 10 November 1989.

Research Notes

Mass Mortality of the Reef Coral *Pocillopora* on the South Coast of Baja California Sur, Mexico

Wilson (1988) reported a geographic range extension for the reef coral *Pocillopora* from its well-known occurrence in the Bahía Pulmo area of the southern Gulf of California to Cabo San Lucas, the cape separating the Gulf from the Pacific Ocean. His note was based on observations made in February 1988, at which time the coralla appeared to be luxuriantly healthy except for lack of zooanthellae ("bleaching") at the tips of many coralla (Wilson, 1988, fig. 3).

Revisitation of the area in July 1989 disclosed that at least 95% of the *Pocillopora* spp. coralla at Punta Palmillas were dead and overgrown with encrusting organisms (bryozoans, worms, barnacles, several kinds of algae). Many of even the largest coralla were nearly unrecognizable. A granite outcropping on the sandy beach formerly covered by *Pocillopora* spp. coralla (Wilson, 1988, figs. 4, 5) was scoured to the rock surface and showed no evidence of former encrustations.

Similar conditions existed at Cabo San Lucas, where an estimated 70% of the *Pocillopora* spp. coralla at Wilson's 1988 locality were dead and covered by encrusting organisms (Fig. 1), including barnacles up to 2 cm in diameter.

At Bahía Pulmo, *Pocillopora* spp. coralla were estimated to be about 10% dead in 5-7 m depths of open areas, perhaps not an abnormal percentage (Hector Reyes, personal communication). However, more than 50% were dead in 3 m depth in the protected rocky cove at the south end of the bay (Fig. 2) by my estimate.

Coralla of other genera (*Pavona*, *Porites*, *Tubastrea*) observed at these localities by me appeared to be healthy.

Reasons for this mass mortality were not apparent. Although large building projects (hotels, condominiums) and dredging contributed to an increase in suspended sediment and other pollution in the Punta Palmillas and Cabo San Lucas areas, the lack of commercial development at Bahía Pulmo indicates another cause for the mortality. If extreme water temperature changes such as reported for the area by Klimley and Butler (1988) are the cause, as suggested by the apparent gradient of increasing mortality from deeper to shallower waters at Bahía Pulmo, then coralla of only one genus would appear to be sensitive to it.

A number of corallivores are known to feed on *Pocillopora*. Moyer, Emerson, and Ross (1982) reported the gastropod *Drupella rugosa* to be selectively destroying coralla of some genera, including *Pocillopora*, in the western Pacific. Glynn and Wellington (1983) cited the echinoid *Eucidaris thouarsii* as grazing in large numbers on live coralla of *Pocillopora* in the Galapagos Islands and also reported predation by two species of hermit crabs, four species of mollusks, two species of starfish (including the infamous *Acanthaster planci*), and several species of fish. Of these, I observed only the gastropod *Quoyula madreporarum* in moderate numbers on coralla of *Pocillopora*, but this species is thought to remain near its attachment scar and do little damage to the coral (Glynn and Wellington, 1983).

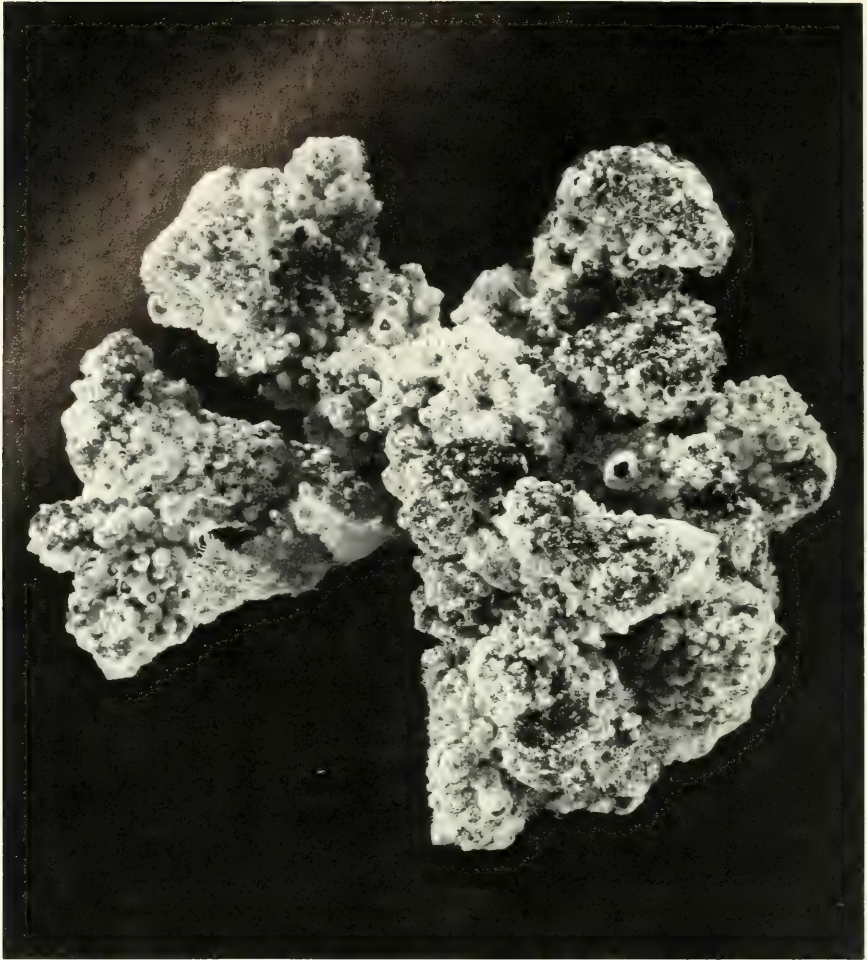


Fig. 1. Fragment from a dead, heavily encrusted corallum of *Pocillopora* sp. collected in July 1989 at Cabo San Lucas. $\times 0.6$.

I saw a few specimens of the corallivore pufferfish *Arothron meleagris* swimming near *Pocillopora* heads in Bahía Pulmo, but not in numbers that could account for the deaths of entire coralla, although they may be responsible for the “bleached” tips. Absence of unusual numbers of corallivores and lack of destruction of delicate calicular structures in the coralla observed by me seems to rule out corallivores as a cause of the mass mortality.

Despite ready accessibility (e.g., Punta Palmillas is a 15 minute drive on paved highway from the international airport near San José del Cabo), reef corals of the area have attracted few researchers. Indeed, all aspects of reef biology and ecology in this region need to be investigated. Increasing building programs may threaten the existence of reef organisms in places.

I am grateful to M. en C. Oscar Arizpe C., Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, for providing transportation and a boat at Bahía Pulmo, official permission for the examination and collection,

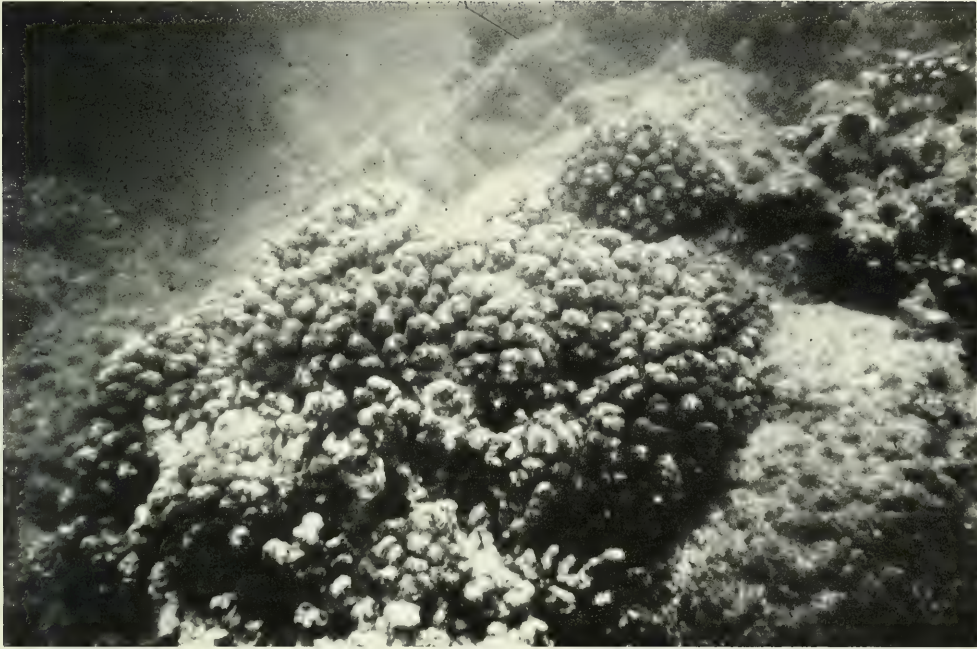


Fig. 2. Underwater view taken in July 1989 of mostly dead coralla of *Pocillopora* spp. in cove at south end of Bahía Pulmo.

and selection of areas to dive there. Sr. Hector Reyes B., who is studying the reef corals at Bahía Pulmo, generously shared his observations on present and past conditions there. Several observers assisted with the underwater survey in addition to M. en C. Arizpe and Sr. Reyes: Dr. Shelton Applegate, Dr. Judith T. Smith, Mr. Jamie Smith, and Sr. Paulino Perez G. I am grateful to them all. Everyone except Sr. Perez dived at Bahía Pulmo; all but Dr. Applegate and M. en C. Arizpe dived at Punta Palmillas; Cabo San Lucas was examined by Sr. Perez, Sr. Reyes, and myself.

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Accepted for publication 12 September 1989.

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Prevalence of Larval Cestodes (*Mesocestoides* sp.) in the Western Fence Lizard, *Sceloporus occidentalis biseriatus* (Iguanidae), from Southern California

Mesocestoides is a cosmopolitan genus of cyclophyllidean cestodes for which the complete life cycle is still unknown. There is a unique larval form, the tetrathyridium, which is commonly found in mammalian, avian, and reptilian intermediate hosts, and which is readily infective to predatory definitive hosts (Schmidt 1986). Presumably, the first intermediate host is an arthropod; however, this has not been proven (Webster 1949). Tetrathyridia have been reported from a wide variety of North American lizards (Telford 1970; Dyer 1971; Mankau and Widmer 1977; Conn and Etges 1984; Goldberg 1985, 1987; McAllister 1988). These reports present infection prevalences for a species at a point and place in time. To our knowledge, infection prevalences over time have not been studied. Such data in addition to data on range, distribution, food habits and natural history of intermediate hosts are necessary if we are to understand the life cycle of this parasite. In this note we give data on yearly prevalences of *Mesocestoides* sp. in western fence lizard, *Sceloporus occidentalis biseriatus*, populations from southern California. *Mesocestoides* sp. has previously been reported in western fence lizards by Voge (1953), Specht and Voge (1965) and Telford (1970).

Western fence lizards were collected by noosing from three localities in Los Angeles County, California: (1) Puente Hills, Whittier (34°01'N, 117°57'W; elevation 150 m); (2) junction California 39 and Crystal Lake Road, San Gabriel Mountains (34°18'N, 117°50'W; elevation 1584 m), and (3) Strawberry Peak off California 2, San Gabriel Mountains (34°17'N, 118°07'W; elevation 1878 m). Numbers of lizards collected by year and site are given in Table 1. The lizards were fixed in neutral buffered 10% formalin and stored in alcohol prior to examination.

Two of the 865 western fence lizards examined contained tetrathyridia of *Mesocestoides* sp. Sections of infected organs were embedded in paraffin, sectioned at 6 μ m and stained with hematoxylin followed by eosin counterstain. Representative specimens were deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA; accession numbers 80795, 80796).

One infected lizard was an adult male (13.9 g; 76 mm snout-vent length (SVL)) collected 11 March 1989 at Strawberry Peak. In this lizard, white cysts containing tetrathyridia were attached to the stomach, intestines, testes, and liver. It was common to find two or three tetrathyridia within a single cyst. In all cases the holdfast was invaginated. Encapsulated tetrathyridia averaged 828 μ m in diameter and contained calcareous corpuscles (Fig. 1) which are characteristic of larval cestodes (Chitwood and Lichtenfels 1972). In addition, 16 tetrathyridia were found free in the coelomic cavity. The second infected lizard was collected in the Puente Hills 15 March 1989. It was an immature male (3.8 g; 47 mm SVL). Thirty-two tetrathyridia were found in the coelomic cavity; none were attached to organs. Prevalence of infection in western fence lizards examined here was 2/865 (0.2%). For 1989, the only year in which *Mesocestoides* sp. was found, prevalence in the

Table 1. Yearly samples of western fence lizards.

	Whittier	Crystal Lake	Strawberry Peak
1971	85	74	—
1972	241	172	—
1986	45	67	—
1987	18	32	—
1988	7	—	15
1989	54	—	55
Totals	450	345	70

Puente Hills population was 1/54 (1.9%) and 1/55 (1.8%) for the Strawberry Peak population.

Our data shows that *Mesocestoides* sp. is uncommon in the western fence lizard in southern California. Its absence in the years 1971–72, 1986–88 indicates it is an infrequent parasite in the western fence lizard populations in the above three study areas.

Twenty-six species of North American lizards have been reported as hosts of *Mesocestoides* sp. tetrathyridia with an additional three species possibly containing them (Table 2). *Sceloporus jarrovi* represents a new host record. For a cosmopolitan genus, *Mesocestoides* sp. has been found in lizards in only a few locations; 7 states but only 15 counties. Reported prevalences ranged from 0 to 27. In addition to the absence of *Mesocestoides* sp. from *Gambelia wislizenii*, Mankau and Widmer (1977) reported its absence from three species of *Sceloporus* (Table 2). The higher prevalences are associated with iguanid lizards of arid habitats

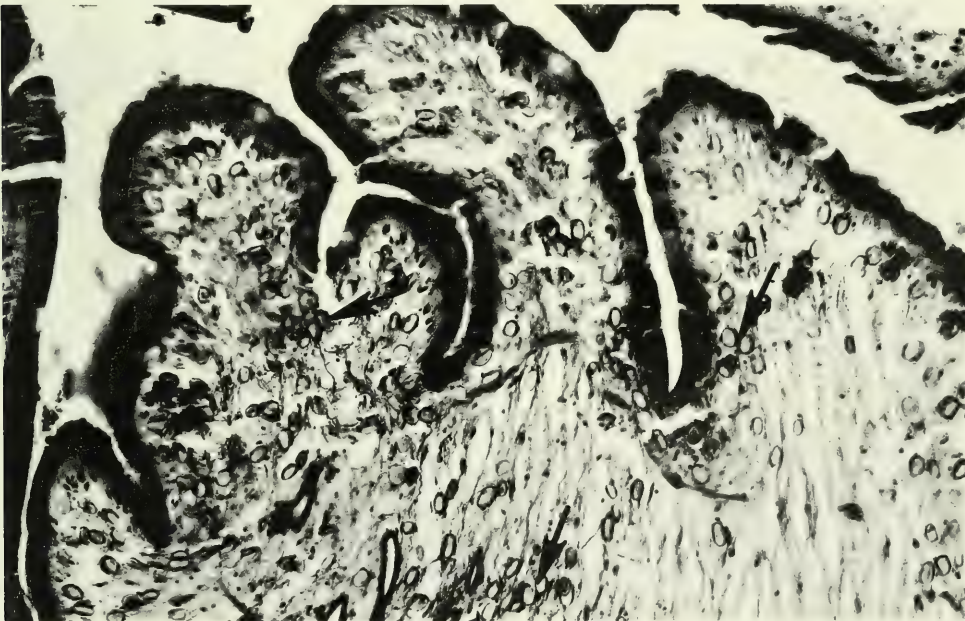


Fig. 1. Histological section through part of a tetrathyridium from the western fence lizard. Note convoluted border and scattered calcareous corpuscles (arrows) which are diagnostic of larval cestodes, 160 $\times$.

Table 2. Prevalences of *Mesocestoides* sp. tetrathyridia in North American lizards.

Lizard species	Num- ber exam- ined	Num- ber in- fec- ted	%	Location: state; county	Reference
Gekkonidae					
<i>Coleonyx variegatus</i>	13	1	8	California: Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
Xantusiidae					
<i>Xantusia riversiana</i>	78	3	4	California: Los Angeles	Telford 1970
<i>Xantusia riversiana</i>	279	5	2	California: Los Angeles	Goldberg 1985
Iguanidae					
<i>Anolis carolinensis</i>	543	2	<1	Louisiana: St. John the Baptist	Conn and Etges 1984
<i>Callisaurus draconoides</i>	25	1	4	*California: San Bernardino and/or Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Callisaurus draconoides gabbi</i>	19	1	†	California: Riverside	Telford 1970
<i>Cophosaurus texanus texanus</i>	21	1	5	Texas: Johnson	McAllister 1988
<i>Crotaphytus collaris</i>	144	29	20	New Mexico: Lincoln	Pfaffenberger <i>et al.</i> 1986
<i>Dipsosaurus dorsalis</i>	63	1	2	*California: San Bernardino and/or Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Gambelia wislizenii</i>	10	0	0	*California: San Bernardino and/or Imperial, Riverside	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Phrynosoma m'calli</i>	15	4	27	California: Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Phrynosoma platyrhinos</i>	11	3	27	*California: San Bernardino and/or Imperial, Los Angeles	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Phrynosoma platyrhinos</i>	104	11	11	Nevada: Clark, Nye	Mayhew pers. comm.
<i>Sceloporus graciosus</i>	29	0	0	*California: Los Angeles and/or Riverside	Babero and Kay 1967 Mankau and Widmer 1977; Mayhew pers. comm.

Table 2. Continued.

Lizard species	Num- ber exam- ined	Num- ber in- fected	%	Location: state: county	Reference
<i>Sceloporus graciosus</i> <i>vandenberghianus</i>	71	1	1	California: Riverside	Telford 1970
<i>Sceloporus jarrovi</i>	489	15	3	Arizona: Pima	Goldberg and Bursley unpublished
<i>Sceloporus magister</i>	26	0	0	*California: Los Angeles and/or San Bernardino	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Sceloporus magister magister</i> **	52	1	2	Arizona: Maricopa	Benes 1985
<i>Sceloporus occidentalis</i>	—	1	—	California: Alameda	Voge 1953
<i>Sceloporus occidentalis</i>	—	—	—	California: Los Angeles, Riverside	Specht and Voge 1965
<i>Sceloporus occidentalis</i>	865	2	<1	California: Los Angeles	This study
<i>Sceloporus occidentalis</i>	45	0	0	*California: Riverside and/or San Bernardino, Los Angeles	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Sceloporus occidentalis</i> <i>biseriatus</i>	116	1	1	California: Riverside	Telford 1970
<i>Sceloporus olivaceous</i>	7	1	14	Texas: Johnson	McAllister 1988
<i>Uma inornata</i>	10	2	20	California: Riverside	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Uma notata</i>	12	1	8	California: Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Uma scoparia</i>	39	2	5	California: San Bernardino	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Urosaurus graciosus</i>	33	1	3	*California: San Bernardino and/or Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Urosaurus ornatus linearis</i> **	100	1	1	Arizona: Maricopa	Benes 1985
<i>Uta stansburiana</i>	19	1	5	*California: Riverside and/or Imperial	Mankau and Widmer 1977; Mayhew pers. comm.

Table 2. Continued.

Lizard species	Num- ber exam- ined	Num- ber in- fect- ed	%	Location: state: county	Reference
<i>Uta stansburiana stejnegeri</i>	639	89	14	*California: Riverside, San Bernardino and Imperial	Telford 1964, 1970
<i>Uta stansburiana stejnegeri</i> **	100	7	7	Arizona: Maricopa	Benes 1985
Teiidae					
<i>Chenidophorus burti</i>	52	1	2		Goldberg 1987
<i>Chenidophorus stictogrammus</i>				Arizona: Pima	
<i>Chenidophorus tigris</i>	24	2	8	*California: San Bernardino and/or Imperial	Mankau and Widmer 1977; Mayhew pers. comm.
<i>Chenidophorus tigris</i> **	87	2	2	Nevada: Clark	Babero and Matthias 1967
<i>Chenidophorus tigris septentrionalis</i> **	50	1	2	Arizona: Maricopa	Benes 1985
<i>Chenidophorus sexlineatus</i>	23	2	9	South Dakota: Todd	Dyer 1971
Scincidae					
<i>Eumeces fasciatus</i> **	—	2	—	Texas: Harris	Harwood 1932
<i>Eumeces fasciatus</i>	—	1	—	***	Voge 1953
<i>Eumeces skiltonianus</i>	14	1	7	California: Riverside, Los Angeles	Telford 1964, 1970
<i>Scincella lateralis</i> **	—	2	—	Texas: Harris	Harwood 1932
Anguidae					
<i>Gerrhonotus coeruleus</i>	—	1	—	California: Contra Costa	Voge 1953
<i>Gerrhonotus multicarinatus webbi</i>	30	2	7	California: Riverside, Los Angeles	Telford 1964, 1970

* Data from two or three counties were pooled.

** Possibly *Mesocostoides* sp.

*** Museum collection, locality data not available.

† *Mesocostoides* sp. present, sample not completely examined.

(Table 2) which may suggest that ecology and food habits are important to infection. Most of these lizards are opportunistic feeders which ingest various arthropods. There is no further development in lizards although normal development can resume should a lizard be eaten by a suitable definitive host (Specht and Voge 1965). Further investigation of these lizards would be appropriate. However, until more is known about the life cycle of *Mesocestoides*, lizards would perhaps best be considered as paratenic rather than intermediate hosts.

Acknowledgments

We are grateful to T. A. Bienz for assisting with fieldwork and to W. W. Mayhew for supplying locality data.

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Accepted for publication 26 July 1989.

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COVER: Fragment from a dead, heavily encrusted corallum of *Pocillopora* sp. Compare with cover and page 79 of volume 87 #2. Photo by Edward C. Wilson. (See Page 39.)